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A palaeoecological approach to understanding the past and present of Sierra Nevada, a Southwestern European biodiversity hotspot

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30 **ABSTRACT**

31 Mediterranean mountainous environments are biodiversity hotspots and priority areas in
32 conservation agendas. Although they are fragile and threatened by forecasted global
33 change scenarios, their sensitivity to long-term environmental variability is still
34 understudied. The Sierra Nevada range, located in southern Spain on the north-western
35 European flanks of the Mediterranean basin, is a biodiversity hotspot. Consequently,
36 Sierra Nevada provides an excellent model system to apply a palaeoecological approach
37 to detect vegetation changes, explore the drivers triggering those changes, and how
38 vegetation changes link to the present landscape in such a paradigmatic mountain system.
39 A multi-proxy strategy (magnetic susceptibility, grain size, loss-on-ignition, macroremains,
40 charcoal and palynological analyses) is applied to an 8400-year long lacustrine
41 environmental archive from the Laguna de la Mosca (2889 masl). The long-term ecological
42 data show how the Early Holocene pine forests transitioned towards mixed *Pinus-Quercus*
43 submediterranean forests as a response to a decrease in seasonality at ~7.3 cal. kyr BP.
44 The mixed *Pinus-Quercus* submediterranean forests collapsed drastically giving way to
45 open evergreen *Quercus* formations at ~4.2 cal. kyr BP after a well-known aridity crisis.
46 Under the forecasted northward expansion of the Mediterranean area due to global
47 change-related aridity increase, mountain forests inhabiting territories adjacent to the
48 Mediterranean Region could experience analogous responses to those detected in the
49 Sierra Nevada forests to the Mid to Late Holocene aridification, moving from temperate to
50 submediterranean and then Mediterranean formations.

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53 **Keywords** biogeography, palaeoecology, vegetation, Holocene, submediterranean, fire,
54 conservation, environmental change

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61 1. INTRODUCTION

62 Regions under Mediterranean climate have been identified as biodiversity hotspots (Myers
63 *et al.*, 2000). The Mediterranean basin, in particular, is the most diverse and
64 heterogeneous of these Mediterranean hotspots (Médail and Quézel, 1997, 1999; Myers
65 *et al.*, 2000). However, the spatial distribution of biodiversity within the Mediterranean
66 basin is uneven, mountains having played a key role in the basin's biodiversity spread and
67 survival through time (Manzano *et al.*, 2017; Médail and Quézel, 1997, 1999).
68 Furthermore, the importance of Mediterranean mountain areas is not only linked to their
69 biodiversity, but also to the many critical ecosystem services they provide (Grêt-Regamey
70 *et al.*, 2010; Körner, 2004; Meybeck *et al.*, 2001; Woodwell, 2004). Unfortunately, both the
71 fragile mountain environments and the services they provide are threatened due to the
72 present trends of unprecedented environmental change and the large anthropogenic
73 pressure they experience (Díaz *et al.*, 2003).

74 In Mediterranean mountains, climate-controlled vegetation belts provide niches for
75 the coexistence of mediterranean, submediterranean and temperate taxa within a single
76 massif (Blanca, 2000). However, belt boundaries are flexible to environmental change
77 (Gabherr *et al.*, 2010; Nagy and Gabherr, 2009) and, consequently, Mediterranean
78 mountainous environments are fragile and their conservation a global concern (Díaz *et al.*,
79 2003; Grêt-Regamey *et al.*, 2010; Körner, 2004; Meybeck *et al.*, 2001; Woodwell, 2004).
80 Under the current global change scenario, mountain conservation issues should consider
81 long-term ecological approaches that provide information on the responses that past
82 vegetation belts had to environmental change (Willis and Bhagwat, 2010; Willis *et al.*,
83 2007). In this sense, Mediterranean mountain environments provide the ideal setting to
84 explore complex biological interactions and vegetation trends through time (Carrión *et al.*,
85 2002, 2007, 2010; Vogiatziakis, 2012). However, the sensitivity of well-preserved
86 Mediterranean mountain environments to long-term environmental variability is still
87 understudied (Díaz *et al.*, 2003).

88 The Sierra Nevada range (S Iberia) is one of the highest mountain ranges in
89 Europe. Its heterogeneous geology, physiography and palaeoecological history are
90 responsible for Sierra Nevada being the western Mediterranean's most important
91 biodiversity hotspot (Blanca, 2000; Lorite, 2016). It was declared a UNESCO Biosphere
92 Reserve in 1986, a Natural Park in 1989, and a National Park in 1999 (Gómez-Ortiz *et al.*,

2005). Sierra Nevada houses ~30% of the Iberian and ~20% of the European flora, covering all European floristic elements and biotypes (Blanca, 2000; Blanco *et al.*, 2005; Lorite, 2016). Therefore, Sierra Nevada is an ideal setting for understanding the effect that long-term environmental changes have on biodiverse Mediterranean mountain settings and how these environmental changes relate to the present structure and distribution of plant biodiversity.

Sierra Nevada's Holocene environmental and landscape changes are nested within the wider western Mediterranean Holocene climatic trends (Anderson *et al.*, 2011; Carrión, 2002; Fletcher and Sánchez-Goñi, 2008; Jalut *et al.*, 2009; Jiménez-Espejo *et al.*, 2014; Jiménez-Moreno and Anderson, 2012; Jiménez-Moreno *et al.*, 2013; Ramos Román *et al.*, 2016, 2018). Both astronomical forcing (i.e., changes in precession and solar irradiance; Bard *et al.*, 2000; Laskar *et al.*, 2004) and internal modes of climate variability (i.e., North Atlantic Oscillation; Trouet *et al.*, 2009; Olsen *et al.*, 2012) have been identified as the modellers of Sierra Nevada landscapes (Anderson *et al.*, 2011; Ramos-Román *et al.*, 2016). Briefly, the Early Holocene has been reconstructed as a humid phase (Anderson *et al.*, 2011; Jiménez Espejo *et al.* 2014; Jiménez-Moreno *et al.*, 2015). This humid phase is followed by an increase in aridity related to a decrease in seasonality, with superimposed drier spells, since ~7 cal. kyr BP (Carrión, 2002; Fletcher and Sánchez-Goñi, 2008; Jiménez-Espejo *et al.*, 2014). After the Mid-to-Late Holocene (~5-4.2 cal. kyr BP) more intense aridity pulses, it seems that the NAO variability is the main driver of vegetation change in Sierra Nevada, as it affected the winter-autumn storm tracks in S Iberia (Ramos-Román *et al.*, 2016). Sierra Nevada current vegetation singularity is outstanding (Rivas Martínez, 1987; Valle, 1985, 2003). In addition, palaeoecological studies show the existence of a variety of vegetation responses to factors such as altitude and aspect (Anderson *et al.*, 2011; Jiménez-Moreno and Anderson, 2012; Jiménez-Moreno *et al.*, 2013; Ramos Román *et al.*, 2016, 2018) that could be behind the present Sierra Nevada singularity. However, the long-term ecological picture of Sierra Nevada is far from complete. New palaeoecological records are needed to fill the gaps in the available information of this unique Mediterranean mountain system in order to bridge Quaternary proxy data with contemporaneous information and merge them into useful, extrapolable models.

Here we present a high-resolution, multi-proxy palaeoecological record of the Sierra Nevada high-altitude Laguna de la Mosca lacustrine site (2889 masl) using palynological, charcoal, macroremains, magnetic susceptibility, loss-on-ignition, and grain size analyses.

127 The aims of the environmental reconstruction of this paradigmatic western Mediterranean
128 mountain setting are i) to detect landscape changes during the Holocene, ii) to explore the
129 drivers triggering those past landscape changes, and iii) to link the detected past
130 environmental changes to the present biodiversity of Sierra Nevada landscapes. This is of
131 special interest in providing retrospective examination for events shaping the present-day
132 diverse Sierra Nevada landscape. Furthermore, the palaeoecological reconstruction of the
133 vegetation assembly and succession during the well-known S Iberian Holocene
134 aridification trend (Anderson *et al.*, 2011; Carrión, 2002; Carrión *et al.*, 2003, 2010) could
135 be used as an analogous for the future response of forest vegetation to the projected
136 northwards expansion of the European Mediterranean climate area within the global
137 change scenario.

138 2. MATERIAL AND METHODS

139 2.1 Regional, physical and environmental setting

140 The Sierra Nevada mountains are in the Baetic Ranges at the south-eastern corner of the
141 Iberian Peninsula (Fig. 1a). Covering 90 km in length, Sierra Nevada runs E-W, parallel to
142 the coast, housing the highest Iberian peaks. Metamorphic siliceous rocks (mica schists)
143 are dominant at the central part of the massif; to the south and west, the massif is framed
144 by calcareous materials such as limestone and dolomite (Delgado Calvo-Flores *et al.*,
145 2001; Fig. 1b). Sierra Nevada was extensively glaciated during the last glacial maximum
146 (LGM). Evidence for LGM glaciers spanning over 2000-2200 masl and 2300-2400 masl is
147 found on the north and south faces of the mountains, respectively (Palacios *et al.*, 2016).

148 Sierra Nevada vegetation is distributed along an altitudinal gradient and affected by
149 bedrock, determining the development of different soil types (Molero Mesa *et al.*, 1992;
150 Fig. 1c). On the detritic, alkaline materials surrounding the massif, open *Pinus halepensis*
151 woodlands with *Pistacia lentiscus*, *Phillyrea angustifolia* and *Retama sphaerocarpa*
152 dominate the thermomediterranean belt (<700 masl; Valle 1985, 2003). *Quercus rotundifolia*
153 dominates the meso- and supramediterranean belts (700-1900 masl), with an understory
154 of Cistaceae (i.e., *Cistus*, *Helianthemum*, *Fumana*) and woody Lamiaceae (i.e.,
155 *Rosmarinus officinalis*, *Salvia*, *Thymus*, *Teucrium*). Scattered stands of *Quercus faginea*
156 appear in the supramediterranean belt, sometimes with *Acer opalus* ssp. *granatense*. In
157 the oromediterranean belt (>1800-1900 masl), sparse pinelands of *P. sylvestris* ssp.
158 *nevadensis* and *P. nigra* ssp. *salzmanii* alternate with a creeping scrub of *Juniperus sabina*
159 and *J. communis* ssp. *hemisphaerica*, frequently as part of a thorny matorral. On

160 dolomites, important in the western areas, edaphic restrictions hamper the development of
161 forests. *P. pinaster* ssp. *acutisquama*-*J. phoenicea/oxycedrus* assemblages dominate the
162 landscape with *P. halepensis* replacing *P. pinaster* in the lower altitude, more thermic and
163 xeric enclaves. Individuals of *P. nigra* ssp. *salzmannii* populate the higher elevation areas
164 (Valle, 1985, 2003).

165 On siliceous substrates, the mesomediterranean belt (700-1500 masl) is dominated
166 by *Q. rotundifolia* and *Q. coccifera* (on arid enclaves) with an understorey of *R.*
167 *sphaerocarpa*, *Cytisus fontanesii*, *C. grandiflorus*, and Cistaceae (i.e., *Cistus*
168 *monspeliensis*, *C. salviifolius*). In the supramediterranean (1500-1900 masl), the
169 evergreen oak formations incorporate *Adenocarpus decorticans* in the understory.
170 However, in altered sites a thorny matorral of *Cotoneaster granatensis*, *Berberis hispanica*,
171 *Crataegus monogyna*, *Prunus ramburii*, and *Rosa* sp. become abundant. Scattered within
172 this vegetation belt, *Q. pyrenaica* groves mark the timberline, sometimes enriched by
173 *Sorbus aria*, *Acer opalus* ssp. *granatense* and *Fraxinus angustifolia*, and more rarely with
174 *Betula pendula* ssp. *fontqueri* and *Salix caprea* (Valle, 1985, 2003). The treeless
175 oromediterranean belt (2700-3000 masl) is covered by pastures as well as prostrated and
176 cushion-like shrubs. It is noteworthy the *Genista versicolor-Juniperus communis* ssp. *nana*
177 community, and the sparse scrub in altered and pronounced slopes dominated by woody
178 Brassicaceae (*Hormatophylla spinosa*, *Vella spinosa*), *Arenaria pungens* ssp. *pungens*,
179 *Reseda complicata* and *Sideritis glacialis* (Valle, 1985, 2003). Patchy waterlogged
180 pastures (locally called *borreguiles*) develop in small depressions and over impermeable
181 soils. They are dominated by mosses and sedges and incorporate many singular floristic
182 elements like *Plantago nivalis*, *Aconitum nevadensis* or *Potentilla nevadensis* (Lorite *et al.*,
183 2003). The highest altitudes comprised in the cryoromediterranean belt (>2700-3000 m),
184 are vegetated by sparse pastures of great floristic endemism dominated by *Festuca*
185 *clementei*, *Nevadensia purpurea*, *Leontodon boryi*, *Viola crassiuscula*, *Herniaria boissieri*,
186 *A. pungens* ssp. *pungens*, *A. tetraquetra* and *Linaria glacialis* (Fernández-Calzada, 2007;
187 Fernández-Calzada and Molero Mesa, 2011).

188 2.2 Sediment sampling

189 Linked to the past glacial history of Sierra Nevada, around 42 permanent lakes are found
190 above 2600 masl. One of them is the Laguna de la Mosca (LdIMo, 2889 masl, 37° 3.58' N,
191 3° 18.88' W; Fig. 1), a small lake with a maximum depth of 3.4 m, a surface of 0.48 ha,
192 and a drainage area of 39.7 ha. LdIMo is located in the foot of the north-facing Mulhacén

193 cirque on metamorphic mica schists. The lake sits above the modern treeline, in the
194 cryoromediterranean belt (Fig. 1). Two sediment cores were retrieved from the lake bottom
195 using a floating platform in September 2013. A 190-cm long sediment core was collected
196 using a Livingston corer. A short core of 20 cm was sampled using a universal corer
197 (Aquatic Research Inc.). The latter core was extracted to avoid the potential mixing of the
198 less compacted upper sediment layers from the former core.

199 **2.3 Palaeoecological analyses and radiocarbon dating**

200 Sixteen samples from the long sediment core were selected for AMS radiocarbon dating
201 (Table 1). One date (AD 1963) was extracted from a ICP-MS Plutonium profile built on the
202 top 15 cm of the short core (Table 1). Radiocarbon dates were calibrated with the
203 IntCal13.14C calibration curve (Reimer *et al.*, 2013), and used together with the Pu date
204 and AD 2013 as the top of the sediment record in order to build an age-depth model (Fig.
205 2) This model was built to include the maximum number of radiocarbon dates possible,
206 excluding the reversal dates (Telford *et al.*, 2004). In total, six dates were identified as
207 outliers (*sensu* Bronk Ramsey, 2009; Christen, 1994) and not included in the age-depth
208 model (Table 1, Fig. 2). Classical, linear interpolation modelling was preferred to
209 polynomial/logarithmic or Bayesian modelling acknowledging its limitations and favouring
210 future improvement (Manzano *et al.*, 2018). The composite sequence was built based on
211 the coherence of the age-depth models of the short and long cores discarding an
212 overlapping section of 3 cm from the top of the long core.

213 **Magnetic susceptibility** (MS; Sandgren and Snowball, 2001) was measured using
214 a Bartington MS2E meter with readings every 5 mm in the long core. No MS
215 measurements were obtained from the short core. **Loss-on-Ignition** (LOI) and **grain size**
216 **distribution** were analysed in 44 samples. LOI was measured after combustion at 450 °C
217 for 4 hours (Davies, 1974). Grain size distribution was obtained using a Coulter LS230
218 laser diffraction particle size analyser after the pre-treatment of the samples with sodium
219 hexametaphosphate and water, as well as mixing in an ultrasonic bath.

220 **Palynological analysis** was performed every 2.5 cm on 0.5 cm-thick samples (75
221 samples) in the long core, and every 1 cm on 0.5 cm-thick samples in the short core (15
222 samples). Samples were processed according to Faegri and Iversen (1989), including
223 density separation following Erdtman (1979). *Lycopodium* tablets were added to the
224 samples at the onset of the process in order to calculate concentrations (Stockmarr, 1971).
225 Palynological counting and identification (×400-1000 magnification) were assisted by the

226 Universidad de Murcia's palynological reference collection, as well as keys and atlases
227 (Díez *et al.*, 1987; Faegri and Iversen, 1989; Moore *et al.*, 1991; Reille, 1992, 1995; Sáenz
228 Laín, 1982; Ruiz del Castillo, 1988). Vascular plant taxonomy follows Flora Ibérica
229 (www.floraiberica.es), if not possible, Flora Europaea or, when the author is indicated, the
230 original species publication. Non-pollen palynomorphs (NPP) nomenclature follows van
231 Geel (2001). The pollen sum consisted of an average of 285 upland pollen grains (trees,
232 shrubs and herbs), and just in an exceptional case a minimum sum of 200 upland pollen
233 grains was attained (25 cm depth). Due to the local presence of woody Brassicaceae
234 (*Hormatophylla spinosa* and *Vella spinosa*), Brassicaceae taxa were considered shrubs
235 rather than herbs. Percentages of all taxa were calculated on the basis of the upland
236 pollen sum. **Microcharcoal** particles were counted on the palynological slides following
237 Finsinger *et al.* (2004) and Mooney and Tinner (2010). The pollen diagram was zoned in
238 four zones using Cavalli-Sforza chord distance based CONISS analysis. Only taxa with
239 percentages >5% were included in the analysis. Zonation analysis and diagram plotting
240 were performed using Tilia (Grimm, 1991). Complete pollen diagrams plotted by age and
241 by depth can be found in supplementary material.

242 Arthropod, seed and charcoal **macroremains** were extracted in 160 samples after
243 deflocculating 1 cm³ of sediment in tetrasodium pyrophosphate and sieving through 250
244 and 125 µm meshes. Counting and identification were performed at ×25-50 magnification.
245 No macroremains were recovered in the top 5 cm.

246

247 **3. RESULTS**

248 **3.1 Lithology, sediment accumulation rates, and records of grain size, LOI and** 249 **magnetic susceptibility**

250 According to the age-depth model, the LdlMo sediments, alternating clays and sandy
251 clays, started to accumulate at ~8.4 cal. kyr BP (Fig. 2). Sediment accumulation rates
252 (SAR) are highest before ~7.3 cal. kyr BP (82 cm), with an overall decreasing trend
253 afterwards. The MS record shows high variability throughout the whole sequence (Fig. 2).

254 The onset of the LdlMo sedimentary sequence is characterised by a rise in mean
255 grain size, reaching 65 µm. This is coeval to a peak in LOI that precedes a progressive
256 decrease spanning to the top of the zone LdlMo-1 (Fig. 2). Values of LOI and grain size
257 smoothly decrease until ~4.2 cal. kyr BP. Between ~4.2 and ~1.4 cal. kyr BP, grain size

mean and LOI show two distinct episodes. Grain size increases from 71 to 85 μm , and LOI from 1 to 2%. Grain size, then, exhibits a gradual decrease followed by another steep rise at ~1.7 cal. kyr BP, when LOI rises from 1 to 8% (Fig. 2). During the last millennium, grain size displays a see-saw pattern while LOI displays a single maximum at 500 cal. yr BP and decreases towards the top of the sequence.

3.2 Palynological, charcoal and macroremains records

The **zone LdlMo-1** (~8.4-7.3 cal. kyr BP; 189-94 cm) shows the highest arboreal percentages for the whole record (Fig. 3). It registers the largest presence of *Pinus sylvestris/nigra* type (up to 60%), *P. halepensis/pinea* type, *P. pinaster* and *Betula*. Shrubs present low values, with *Juniperus* and *Cytisus/Genista* type as the most important shrubby types. Poaceae dominates the herbaceous assemblage, which also shows a significant presence of Caryophyllaceae, with recurring peaks in the percentages of *Herniaria* and *Spergularia* (Fig. 3). Cyperaceae and *Botrychium lunaria* are the most abundant types of the hygro-hydrophyte component, which is poorly developed (Fig. 3). The percentages of Zygnemataceae, and the concentrations of seeds and *Daphnia* eggs are fluctuant. The macro- and microcharcoal influx records show see-saw patterns (Fig. 3).

The **zone LdlMo-2** (~7.3-4.2 cal. kyr BP; 94-49 cm) is characterised by landscape stability. *Pinus* (~25%) and *Quercus* (5-10%) percentages remain constant, whereas *Quercus suber* displays the largest values in the whole record (Fig. 3). This zone shows the vanishing of the pollen signal of mesophytic taxa such as *Castanea* (at ~7 cal. kyr BP), *Corylus* (at ~5 cal. kyr BP) and *Betula* (at ~4.5 cal. kyr BP). *Cytisus/Genista* type percentages show decreasing values coeval to the increasing values of the *Juniperus*-Brassicaceae assemblage (Fig. 3). The herbaceous component shows increasing values, commanded by Poaceae, Caryophyllaceae and *Herniaria*, together with Chenopodiaceae, Ranunculaceae and *Artemisia* (Fig. 3). The microcharcoal influx record displays low, constant values contrasting with the oscillating values displayed by the macrocharcoal influx record. However, the top of the zone shows a peak in the microcharcoal influx (Fig. 3). Lacustrine vegetation is better represented in this zone than in the previous one, with larger values of Cyperaceae, Alismataceae and *Potamogeton* (Fig. 3). The upland vegetation stability contrasts with the algal fluctuations. Zygnemataceae peaks are coeval with those in Chrysophyceae, *Anabaena* and Cladoceran heads (Figs. 2 and 3).

The **zone LdlMo-3** (~4.2-1.1 cal. kyr BP; 49-18 cm) shows low arboreal percentages, with a significant decrease in the values of *P. sylvestris/nigra* type, *P.*

291 *halepensis/pinea* type and deciduous *Quercus* (Fig. 3). However, evergreen *Quercus*
292 shows similar values than in the previous zone. The *Q. suber* signal disappears at ~1.8
293 cal. kyr BP. *Juniperus*, *Cytisus/Genista* type and Brassicaceae are the most represented
294 shrubby taxa. Mediterranean thermophytes and drought-tolerant taxa (i.e., *Phillyrea*,
295 Lamiaceae, *Ephedra fragilis* type, *Daphne gnidium* type and Cistaceae) are more
296 prevalent from ~3 cal. kyr BP onwards (Fig. 3). Poaceae dominates the herbaceous
297 component, peaking at the onset of the zone and slowing decreasing its values towards
298 the top of the zone while Caryophyllaceae percentages show increasing values. *Artemisia*
299 becomes frequent, with average values of ~10%. Other herbaceous types such as
300 Cichorioideae, *Aster* type, Chenopodiaceae and Ranunculaceae, are also more prevalent.
301 The wetland assemblage (e.g., Cyperaceae, *Pteridium aquilinum* and scattered
302 occurrences of *Potamogeton*, *Anabaena* and Zygnemataceae) lowers its importance (Fig.
303 3). Micro- and macrocharcoal influxes are low, the latter slightly increasing its values from
304 ~2 cal. kyr BP, when a larger presence of seeds has also been detected (Fig. 3).

305 The **zone LdIMo-4** (< ~1.1 cal. kyr BP; 18-0 cm) shows an increase in arboreal
306 pollen, mainly due to *P. sylvestris/nigra* type, *Olea* and *Castanea* (Fig. 3). Alpine
307 (*Juniperus*, *Cytisus/Genista* type and Brassicaceae) and thermophytic taxa (*Phillyrea*) also
308 present increasing values. The most prominent feature of the herbaceous stratum in this
309 zone is the see-saw pattern presented by the Caryophyllaceae-*Herniaria-Spergularia*
310 assemblage, which is opposite to the pattern displayed by *Artemisia*. Deciduous *Quercus*
311 vs. evergreen *Quercus/Quercus suber* also present alternating peak patterns (Fig. 3).
312 Cerealia and *Secale* are recorded in this zone. Wetland taxa are represented by
313 Cyperaceae, Alismataceae, *Isoetes* and the local presence of seeds (Figs. 2 and 3).
314 Invertebrate remains show an increasing trend towards the top of the core, with
315 coprophilous fungi following the same trend. Macro- and microcharcoal influx records
316 show low values, the latter increasing abruptly in recent decades (Fig. 3).

317 **4. DISCUSSION**

318 Lacustrine sedimentation and peat accumulation in Sierra Nevada started during
319 the Holocene deglaciation. This is reflected in the oldest dates of available
320 palaeoecological archives in the area, which follow three chronological patterns of
321 sedimentary accretion and peat accumulation likely connected with climate events. The
322 accumulation of lacustrine sediments in the south facing of the mountain massif,
323 exemplified by the Laguna de Río Seco (LdRS) record (3020 masl, Fig. 1), started at

~11.5 cal. kyr BP, the Holocene onset (Anderson et al., 2011). Although lacustrine sedimentation also started during the late Holocene (~8.4-8.5 cal. kyr BP) in the north facing of Sierra Nevada, as shown by the BdIV record (2945 masl, Fig. 1), it was not after ~5.4 cal. kyr BP when peatlands became significant in this area (García-Alix et al. 2012, 2017; Jiménez-Moreno and Anderson, 2012). The LdIMo (this study, 2889 masl, Fig. 1) is in the northern slope of the massif, and the timing of the beginning of the lacustrine sediment accumulation agrees with the previously observed trend in peat accumulation in the BdIV, as the oldest sediments date back to ~8.4 cal. kyr BP. After the complete deglaciation during the Early Holocene and the retraction of the permanent snowline, high sediment accumulation rates show a large environmental dynamism. It is likely that, as reconstructed for the BdIV record, the LdIMo basin was formerly occupied by permanent snow, and it was just when the snow disappeared that environmental archives started to accumulate peat or sediments (Jiménez-Moreno and Anderson, 2012). A third common chronology for the onset of available deposits is detected in both northern and southern slopes of Sierra Nevada. The south facing Borreguiles de la Caldera (BdIC) record (2992 masl, Fig. 1) shows peat accumulation from ~4.5 cal. kyr BP (Ramos-Román et al., 2016), while the north facing Laguna de la Mula (LdIM) record (2497 masl, Fig. 1) presents lacustrine sedimentation from ~4.1 cal. kyr BP (Jiménez-Moreno et al., 2013).

4.1 Long-term vegetation response to environmental change

4.1.1 A wet Early Holocene with increased seasonality and aridity pulses (~8.4-7.3 cal. kyr BP): the importance of high-altitude *Pinus* forests

The maximum extension of pinewoods in the Sierra Nevada is documented by the notable presence of *P. sylvestris/nigra* type during the Early Holocene in the LdRS and BdIV records (Anderson et al., 2011; Jiménez-Moreno and Anderson, 2012), a picture also reconstructed in LdIMo (Figs. 3 and 4). The occurrence of the high-altitude pine forests evidences the Holocene highest elevation of the subalpine treeline in Sierra Nevada. This is supported by pollen rain studies in the Iberian peninsula (Andrade et al., 1994; Dorado and Ruiz-Zapata, 1994; Vázquez and Peinado, 1993) and an ongoing local pollen rain transect that shows the occurrence of *Pinus* pollen percentages of ~40-70% within pinelands (Ramos-Román *in prep*; preliminar results cited in: Ramos Román et al., 2016). The treeline is sensitive to the length of the growing season, hence to temperature. It is likely that increased seasonality during the Early Holocene favoured the continuation of pine forests in many Southern Iberian landscapes (Anderson et al., 2011; Gil-Romera et

357 *al.*, 2010). However, the picture is far from stable. The palaeoecological reconstruction of
358 the LdlMo evidences centennial-scale cold-aridity spells inferred by fluctuations in the
359 *Pinus*-cryoxerophilous highland vegetation assemblage (Fig. 4). Centennial-scale
360 altitudinal displacements of the treeline are observed by the contrasting patterns of *P.*
361 *sylvestris/nigra* type and Caryophyllaceae (likely the cryoxerophilous *Arenaria tetraquetra*
362 and *A. pungens*), *Herniaria* (likely the endemic *H. boissieri*) and *Spergularia* (Fig. 4).
363 During arid pulses, decreasing winter snowpack would have allowed the upward
364 availability of uncovered soils, as reflected by changes in the grain size distribution (Fig.
365 2), triggering the expansion of cryoxerophilous vegetation. Contrastingly, humid periods
366 would have allowed the survival of the permanent snow cover for longer periods,
367 hampering the upslope expansion of the cryoxerophilous pastures and cushion-like scrub.

368 Mediterranean pines (*P. pinea/halepensis* type and *P. pinaster*) occurred in the
369 lowlands during the Early Holocene. The lowlands, however, were dominated by both
370 evergreen and deciduous *Quercus*, as evidenced by the Padul record (Ramos-Román *et al.*,
371 2018), *Quercus* occupying an ecotonal position bridging the lowland and mountain
372 pinelands (Figs. 3 and 4). Mesophilous trees (e.g., *Betula*, *Alnus*, *Corylus* and *Castanea*)
373 probably concentrated in riparian enclaves, and they show an important representation in
374 zone LdlMo-1 (Fig. 3). These riparian trees seem to have tolerated the cold-aridity
375 fluctuations within the overall warm-wet period. A significant part of the water source in the
376 Sierra Nevada mid- and lowlands derives from groundwater discharges (Fernández
377 Escalante *et al.*, 2006). Summer melting and superficial runoff in the upper Sierra Nevada
378 mountains infiltrate through the schist fractures, recharging the underlying aquifers. The
379 resulting groundwater diffuses and forms springs, feeding watercourses and nurturing the
380 lower-elevation vegetation. Therefore, it is likely that the persistence of mesophilous trees
381 to the centennial-scale aridity pulses was mediated by groundwater storage.

382 4.1.2 Mid-Holocene decrease in seasonality and increase in aridity (~7.3-4.2 cal. kyr BP): 383 the development of *Pinus-Quercus submediterranean* forests

384 The Mid-Holocene onset meant a progressive cooling trend due to a decrease in summer
385 insolation (Laskar *et al.*, 2004). A competitive readjustment between *P. sylvestris/nigra*
386 type and evergreen/deciduous *Quercus* is observed in many SW European sites because
387 of the decrease in seasonality (e.g., Carrión, 2002; Carrión *et al.*, 2001, 2003, 2007;
388 Fletcher and Sánchez-Goñi, 2008; Pantaleón Cano *et al.*, 2003). In Sierra Nevada, this is
389 observed from ~7 to 4.5/4 cal. kyr BP in LdRS and BdIV (Anderson *et al.*, 2011; Jiménez-

390 Moreno and Anderson, 2012), and from ~7.3 to 4.2 cal. kyr BP in the LdlMo (Fig. 4). The
391 three palaeoenvironmental sequences record the presence of pine together with a large
392 importance of deciduous *Quercus*, most likely the marcescent *Q. pyrenaica* and *Q.*
393 *faginea*, pointing to the development of submediterranean vegetation in Sierra Nevada
394 (Figs. 4 and 5).

395 The *Pinus-Quercus* submediterranean forests persist during a period that
396 experiences a decrease in humidity. The latter is evidenced by the virtual disappearance
397 of some mesophytic taxa (*Alnus*, *Betula*, *Corylus*), the development of the Brassicaceae-
398 *Juniperus* alpine scrub, and the rising trend in the values of Poaceae and Asteraceae
399 (Figs. 3 and 4). The invasion of the submediterranean forests by evergreen *Quercus* (most
400 likely *Quercus rotundifolia*) is also registered during the aridification trend. Very
401 interestingly, the N and S aspects of Sierra Nevada seem to have responded differently to
402 the generalised Mid-Holocene aridification trend identified for the southern Iberian
403 Peninsula (e.g., Carrión, 2002; Carrión *et al.*, 2001, 2003, 2007; Fletcher and Sánchez-
404 Goñi, 2008; Pantaleón Cano *et al.*, 2003). The millennial-scale persistence of
405 submediterranean *Quercus-Pinus* forests in the N aspect of Sierra Nevada contrasts with
406 a gradual *Pinus* forest decline and *Quercus* forest increase in the S slopes (Anderson *et*
407 *al.*, 2011). The different vegetation responses to the aridification trend is attributed to the
408 probable different species composition in the pinelands of the N and S slopes (see section
409 4.3.1).

410 4.1.3 Late Holocene aridity crisis (< ~4.2 cal. kyr BP) and forest collapse

411 The Late Holocene experienced an aridity crisis, as seen in many SW European
412 environmental reconstructions (e.g., Carrión *et al.*, 2003, 2010; Pantaleón Cano *et al.*,
413 2003). In the specific case of Sierra Nevada, lower lake levels have been inferred in
414 several records (Anderson *et al.*, 2011; Jiménez-Moreno and Anderson, 2012; Jiménez-
415 Moreno *et al.*, 2013; Ramos Román *et al.*, 2016 and references therein). The LdlMo record
416 shows the depletion of snow-favoured alpine and subalpine scrub (Brassicaceae,
417 *Cytisus/Genista* type, *Juniperus*) in favour of Poaceae and *Artemisia* (Figs. 3 and 4),
418 suggesting sparser vegetation in the summit areas (Valle, 1985, 2003). In addition, from
419 ~4.2 cal. kyr BP onwards, the LdlMo record displays a drastic landscape opening
420 manifested by abrupt drops in both arboreal pollen percentages (Fig. 4) and
421 concentrations (Supplementary information 3). This drastic landscape opening happens
422 just after a peak in the microcharcoal influx record (Fig. 4), suggesting higher fire activity

423 triggered by the onset of the Late Holocene aridity crisis. The formerly extensive *Pinus-*
424 *Quercus* submediterranean forest collapsed in Sierra Nevada about four millennia ago
425 (Figs. 4 and 5).

426 After the ~4.2 cal. kyr BP forest collapse much of the thermic domain suitable for
427 trees was probably deprived of soils due to the combination of steep slopes, deforestation
428 and prevailing arid conditions. It is, therefore, expected that the Late Holocene vegetation
429 of the Sierra Nevada highlands acquired a strong edaphophilous character. This is
430 supported by the rising importance in subalpine scrub, alpine elements and xerophytes
431 (Figs. 3 and 4). Late Holocene tree cover would have been restricted to the lowlands only,
432 as well as likely dominated by open forests of the evergreen *Q. rotundifolia* (Figs. 4 and 5,
433 Ramos-Román *et al.*, 2018), with the secondary participation of other trees (i.e., *Quercus*
434 *suber*, *Pinus halepensis*) that occupied favourable positions such as small basins and
435 moister soils.

436 4.1.4 Late Holocene record of human activity

437 The importance of *Rumex*, *Plantago* and *Urtica* since four millennia ago frames the onset
438 of human-favoured taxa. This is evidenced by land-use changes inferred by the larger
439 occurrence of likely cultivated taxa such as *Castanea*, *Olea* and *Cerealia*, as well as of
440 indicators of grazing activities such as coprophilous fungi (Fig. 4). Anthropogenic activities
441 intensify in the last ten centuries, when crops (e.g., *Cerealia*, *Secale*, *Olea* and *Castanea*)
442 are more abundant.

443 Interestingly, crops were not limited to the lowlands, as it has been documented that
444 the cultivation of rye expanded up to 2300 masl (Boissier, 1839-1845). Further impact on
445 the high-altitude landscapes during the last centuries is evidenced by the rise of
446 coprophilous fungi not only in the LdlMo record (Fig. 4), but also in the LdRS and BdIC
447 records (Anderson *et al.*, 2011; Ramos-Román *et al.*, 2016). The chronological frame of
448 this grazing intensification agrees with the recorded evidence of animal husbandry in the
449 late 18th century (Boissier, 1839-1845). However, coprophilous fungi from the onset of the
450 LdlMo sequence (Fig. 4) may indicate that wild game, likely Spanish ibex (*Capra*
451 *pyrenaica*), has inhabited the mountains and used the permanent water points of the
452 Sierra Nevada highlands for the last eight millennia.

453 The landscape opening that started four millennia ago seems to have culminated
454 during the 18th-19th centuries, when the lowest arboreal cover for the last eight millennia is

455 registered (Figs. 3 and 4). In fact, a widely open landscape is pictured in *Voyage dans le*
456 *midi de l'Espagne* (Boissier, 1839-1845). In this first comprehensive geobotanical study of
457 Sierra Nevada, trees are recorded in scattered patches up to ~1900 masl. According to
458 Boissier (1839-1845), monospecific patches of *P. sylvestris*, *Q. pyrenaica* and *Q.*
459 *rotundifolia* overlapped altitudinally, their distribution agreeing with edaphic rather than
460 bioclimatic features. Finally, the 20th century *Pinus* pollen peak (Fig. 4) reflects the
461 widespread afforestation with pines to prevent the soil erosion triggered by the open
462 landscapes of the previous centuries (Arias Abellán, 1981).

463 **4.2 Forest composition and fire links**

464 The LdlMo charcoal influx records show long-term fluctuations (Figs. 3 and 4). These
465 fluctuations are related not only to the fuel load, as shown in Mediterranean landscapes
466 (Gil-Romera *et al.*, 2010, 2014), but also to its spatial distribution (Fig. 5). Thanks to the
467 palaeoecological records recovered from the LdlMo, fire dynamics can be explained by the
468 dominant forest-types that inhabited the mountainous landscape for the last eight
469 millennia. In pine forests, such as the reconstructed at ~8.4-7.3 cal. kyr BP in Sierra
470 Nevada (Fig. 5), the distribution of flammable materials is spatially segregated. Pine
471 remains and resinous litter of difficult degradation accumulate on the ground, separated by
472 'flameproof' trunks from the fire-sensitive crowns (Fernandes *et al.*, 2008; Ordóñez *et al.*,
473 2013). Early Holocene pine forests' wildfires must have occurred most likely as surface
474 fires (Fig. 5), with no major consequences for adult trees (Morales-Molino *et al.*, 2017).
475 Furthermore, surface fires reduce ground-level competition, and they have been observed
476 to promote the establishment of the shade-tolerant *Pinus nigra* seedlings (Ordóñez *et al.*,
477 2004). Thus, recurrent surface fires probably contributed to the postglacial inertia of
478 pinelands in Southern Iberia (Gil-Romera *et al.*, 2010).

479 Mixed submediterranean *Pinus-Quercus* formations (Blanco *et al.*, 2005; Sánchez
480 de Dios, 2004; Sánchez de Dios *et al.*, 2009), contrastingly, produce less flammable litter
481 (Ganteaume *et al.*, 2014). In addition, this less flammable litter is easily decomposed
482 owing to enhanced fungal activity (Conn and Dighton, 2000). From ~7.3 to 4.2 cal. kyr BP,
483 when mixed pine-oak forests are reconstructed in Sierra Nevada (Figs. 4 and 5), the
484 presence of fungal spores is the highest for the entire LdlMo palaeoecological record (Fig.
485 4). In a context of attenuated seasonality, competition for litter between fungal decay and
486 fire explains the low charcoal influx detected during the Mid-Holocene. Although fungal
487 activity would have fuel-depleted the mixed *Pinus-Quercus* formations and, thus,

repressed fire incidence, these formations constitute multi-stratified forests (Sánchez de Dios *et al.*, 2009), hence providing vertical continuity for surface fires to spread into the canopy in case of punctual fires (Fig. 5). In fact, the ~4.2 cal. kyr BP arid spell, that would have likely repressed the fungal activity, must have triggered drastic fire episodes in the LdlMo-2 and LdlM-3 pollen zone boundary (Figs. 4 and 5). Fires, escalating to the canopy, likely triggered an abrupt shift from the mixed submediterranean *Pinus-Quercus* forests to evergreen *Quercus* sparse vegetation, as reconstructed by the forest collapse four thousand years ago (Figs. 4 and 5).

By the Late Holocene, the Sierra Nevada had few forests remaining (Figs. 4 and 5; Anderson *et al.*, 2011; Jiménez-Moreno and Anderson, 2012; Jiménez-Moreno *et al.*, 2013; Ramos Román *et al.*, 2016). Fire incidence, hence, would have been strongly limited by the sparsity of available fuel, as recorded with the low values in charcoal influx (Fig. 4). It is only very recently, in the last centuries, when an intensification of burning is recorded linked to the afforestation with pines and the increasing human impact in the Sierra Nevada mountains (Figs. 4 and 5).

4.3 A palaeoecological perspective to the understanding of the current Sierra Nevada landscape

The Baetic Ranges epitomises a geobotanical puzzle (Rivas Martínez, 1987; Valle, 1985, 2003). A holistic explanation for the extant vegetation of Sierra Nevada has challenged geobotanists for centuries, and several interpretations of its flora and vegetation have arisen from different neontological approaches (Blanca, 2002; Boissier 1839-1845; Clemente, 1804; Losa Quintana *et al.*, 1986; Quézel, 1953; Rivas Goday and Major, 1966; Rivas Martínez, 1987; Valle, 1985, 2003). Here, we attempt a geobotanical explanation integrating our new high-resolution, multi-proxy palaeoecological record in the context of the available floristic, biogeographical, cultural and palaeobotanical information for the area in order to shed light into the occurrence of some of the singular vegetation still thriving in Sierra Nevada.

4.3.1 Southern Baetic *Pinus sylvestris* ssp. *nevadensis* and *Pinus nigra* forests

Sierra Nevada, along with the nearby Sierra de Baza, hosts the world's southernmost *Pinus sylvestris* forests. The Quaternary history of migration and isolation has left morphological (Gaussen, 1960), ecological (Nicola and Gandullo, 1969) and genetic imprint (Prus-Głowacki *et al.*, 2003; Sinclair *et al.*, 1999; Soranzo *et al.*, 2000) in such

520 populations, supporting the classification of an endemic subspecies: *P. sylvestris* ssp.
521 *nevadensis*. However, palaeobotanical micro and macroremains suggest that the most
522 extended pine species during the Last Glacial in the Mediterranean was *P. nigra* (Desprat
523 *et al.*, 2015; Postigo Mijarra, 2010a). The difficulty of identifying pollen grains beyond the
524 *P. sylvestris/nigra* type hinders conclusions about the Holocene composition of Sierra
525 Nevada pinelands. Nevertheless, the Sierra Nevada palaeobotanical data support
526 widespread representation of mountain *Pinus* forests at the Early and Mid-Holocene (this
527 study; Anderson *et al.*, 2011; Jiménez-Moreno and Anderson, 2012).

528 It is unlikely, however, that Late Glacial conditions with a great proportion of the
529 high-altitude zones under permanent snows or glaciers (Gómez-Órtiz *et al.* 2005), left
530 altitudinal breadth for vegetation belt segregation along the steep slopes of Sierra Nevada
531 mountains. Consequently, mixed *P. nigra* and *P. sylvestris* ssp. *nevadensis* would have
532 likely occurred in the lowlands during the cold Late Pleistocene (Menéndez-Amor and
533 Flörschutz, 1962; Pons and Reille, 1988). Although rare, a modern analogue of these
534 hypothetical mixed pinelands occurs at scattered locations, marking the treeline in some
535 areas of the siliceous Iberian Central System. The small mixed patches of *P. sylvestris* and
536 *P. nigra* that mark the timberline in some areas of the Sierra de Gredos are considered the
537 last vestiges of more extended pinelands (Génova *et al.*, 2009). Remarkably, these mixed
538 groves, also display a more open structure with *Q. pyrenaica* taking over the gaps left by
539 collapsing trees. A similar situation might have arisen along the Mid-Holocene in the Sierra
540 Nevada highlands, and recorded in the LdlMo record and the other Holocene
541 palaeoecological records (Fig. 5; Anderson *et al.*, 2011; Jiménez-Moreno and Anderson,
542 2012; Jiménez-Moreno *et al.*, 2013; Ramos Román *et al.*, 2016).

543 The moister conditions of the Early Holocene likely promoted the expansion of *P.*
544 *sylvestris* ssp. *nevadensis* in areas where *P. nigra* was already living. Then, the Mid-
545 Holocene decrease in seasonality and aridity intensification could have triggered a
546 segregation of the mixed pinelands. *P. nigra* likely took over higher, colder and more xeric
547 locations, while *P. sylvestris* ssp. *nevadensis* the lower and moister ones. At a landscape
548 scale, it is probable that *P. sylvestris* dominated in the moister N aspect, and *P. nigra* in
549 the S aspect of the mountains.

550 The Mid-Holocene progressive forest demise and invasion of the pinelands by
551 deciduous *Quercus*, likely *Q. pyrenaica*, triggered a forest transition towards more open
552 mixed *Pinus-Quercus* forests in the northern slope of the Sierra Nevada mountains.

553 However, this invasion of the pinelands by deciduous *Quercus* was limited in the southern
554 slopes, where effective humidity and insolation are more restrictive (Rams Sánchez,
555 2007). This feature is reflected in the magnitude of the deciduous *Quercus* pollen signal in
556 LdlMo (N facing, this study) and LdRS (S facing, Anderson *et al.*, 2011). The different
557 forest composition in the two mountain slopes is also reflected in the different vegetation
558 response to the ~4.2 cal. kyr BP arid event. While in the northern slope mixed, multi-
559 stratified submediterranean *P. sylvestris*-*P. nigra*-*Q. pyrenaica* forests collapsed after a
560 drastic fire event (this study, Figs. 4 and 5), the more xeric southern slope vegetated by *P.*
561 *nigra* formations experienced a progressive decline (LdRS; Anderson *et al.*, 2011).

562 Supporting the role of abrupt fire events in the shift from mixed *Pinus-Quercus*
563 submediterranean forests to open *Quercus* formations, the extant *P. sylvestris* ssp.
564 *nevadensis* woods found in Sierra Nevada survive only in locations where the calcifuge *Q.*
565 *pyrenaica* is excluded, and thus where multi-stratified forests have never developed. The
566 present-day Sierra Nevada pinelands are restricted to the calcareous enclaves in the
567 western areas: the Monachil valley, the Barranco del Espinar and the Cerro del Tesoro
568 between 1600 and 1900 masl (Blanca, 2000; Olmedo-Cobo *et al.*, 2017). The pinelands in
569 the Sierra de Baza, only ~40 km inland, are open forests on metamorphic, siliceous
570 substrates, where deciduous *Quercus* are not lithology-restricted. However, the Baza
571 pinelands are situated at higher altitudes (>1800 masl) where the vegetative period is too
572 short for the development of *Q. pyrenaica* or other broadleaved forests (Gómez Mercado
573 and Valle, 1988). In both cases, *P. sylvestris* ssp. *nevadensis* occupies N facing, moister
574 and cooler stations, while *P. nigra*, marking the timberline, grows in more xeric areas, in
575 isolated, disperse stands.

576 4.3.2 *Quercus pyrenaica* at the treeline

577 The extant submediterranean *Q. pyrenaica* woods in Sierra Nevada are of great floristic
578 and ecological singularity (Vilches de la Serna, 2014), as they include not only the typically
579 submediterranean species such as *Acer opalus* ssp. *granatense*, *Daphne laureola* or
580 *Lonicera arborea* (Sánchez de Dios, 2004) but also Mediterranean ones such as *Cytisus*
581 *scoparius* ssp. *reverchoni*, *Daphne gnidium* or *Quercus rotundifolia* (Lorite, 2008). Under
582 the prevailing and accentuated Mediterranean macroclimate, *Q. pyrenaica* forests
583 represent a marginal formation (Blanca, 2000; Rams Sánchez, 2007). Their location at the
584 timberline in Sierra Nevada is restricted to valleys, and it is explained by edaphic water
585 compensation (Vilches de la Serna, 2014). Soil denudation elsewhere in the Sierra

586 Nevada highlands together with the Late Holocene aridity crisis might have hampered the
587 development of high-altitude forested belts in the N aspect of Sierra Nevada after the ~4.2
588 cal. kyr BP drastic fire event recorded in the LdlMo sequence (Fig. 4).

589 4.3.3 Broadleaved mesophytes and *Cedrus*

590 *Betula*, *Corylus*, *Alnus*, *Castanea*, *Fraxinus*, *Ilex* and *Populus* palaeobotanical
591 microremains appear in Sierra Nevada during the Holocene (this study; Anderson *et al.*,
592 2011; Jiménez Moreno and Anderson, 2012; Ramos-Román *et al.*, 2018) in agreement
593 with the regional mesophytic maximum identified for S Iberia (Carrión, 2002). The
594 presence of *Castanea* is noteworthy before any agricultural evidence in LdlMo, providing
595 additional evidence to the naturalness of *Castanea* in S Iberia (Anderson *et al.*, 2011;
596 Carrión *et al.*, 2008; García Amorena *et al.*, 2007; Morales-Molino *et al.*, 2011; Pons and
597 Reille, 1988). Evidence of the presence of *Juglans* in the nearby ranges can be traced
598 back to the Upper Pleistocene (Carrión and Sánchez Gómez, 1992) albeit pollen evidence
599 from Sierra Nevada only dates as far back as the Mid- to Late Holocene transition (this
600 study, Fig. 3). Its origin, whether cultivated or not, is uncertain.

601 *Cedrus* is recorded in the LdlMo palaeoecological record (Fig. 3). The presence of
602 *Cedrus* in Southern European Mediterranean palaeoenvironmental records has been
603 much debated. Magri and Parra (2002) attribute the detection of *Cedrus* during arid and/or
604 deforested periods to long-distance wind transport from N Africa. Under such
605 circumstances, usually low pollen concentrations are found in the sediments, allowing for
606 an overrepresentation of long-distant taxa (Magri and Parra, 2002). On the one hand,
607 Sierra Nevada palaeoenvironmental data show *Cedrus* pollen after the Late Holocene
608 forest collapse (this study; Anderson *et al.*, 2011), a scenario compatible with Magri and
609 Parra (2002). On the other hand, the presence of *Cedrus* is also detected before the aridity
610 crisis, when forests were extensive (Fig. 3), a scenario not compatible with Magri and
611 Parra (2002). Alternatively, it has been suggested that relict stands of cedars survived
612 hidden in the Baetic Ranges during the Holocene (Postigo-Mijarra *et al.*, 2010b). However,
613 the lack of macroremains in the northern coast of the Mediterranean hampers a definitive
614 conclusion on its Quaternary presence in Iberia (Magri and Parra, 2002).

615 5. CONCLUSIONS

616 The Holocene landscape history of Sierra Nevada has been influenced by climatic,
617 edaphic and anthropogenic drivers. The pine forests that dominated the Sierra Nevada

618 landscape during the Early Holocene were affected by a decrease in seasonality around
619 seven millennia ago. This allowed the proliferation of deciduous and evergreen *Quercus*
620 and the establishment of submediterranean mixed *Pinus-Quercus* forests that dominated
621 the landscape for almost three millennia, between ~7.3 and 4.2 cal. kyr BP. Owing to the
622 different structural complexity of the pine forest vs. the mixed pine-oak forests, the latter
623 responded drastically to the fire activity detected at ~4.2 cal. kyr BP, triggering the collapse
624 of the forest cover in Sierra Nevada. In addition, Late Holocene landscapes were also
625 impacted by agricultural and grazing activities, that intensified in the last centuries. It is
626 also in recent times when pine afforestation increased the forest cover in Sierra Nevada.
627 The scattered forests that inhabit the landscape nowadays rely on soil moisture
628 compensation to survive summer drought. This is the case of the *P. sylvestris* ssp.
629 *nevadensis* pinelands or the *Q. pyrenaica* forests that mark the current timberline. Thus,
630 forest cover in Sierra Nevada has not only climatic and anthropogenic imprints, but it is
631 also marked by a strong edaphic and lithologic influence.

632 Under the current global change scenario, the projected increase of temperatures
633 and subsequent aridification of the Mediterranean will notably affect European landscapes
634 (IPCC, 2013). Forecasts include a northwards expansion of the summer-drought, meaning
635 the spread of Mediterranean-like conditions to new areas (Barredo *et al.*, 2016), including
636 to forested mountains. This means that the mountainous forests inhabiting territories
637 adjacent to the Mediterranean Region could experience analogous responses to those
638 detected in the Sierra Nevada forests to the Late Holocene aridification, moving from
639 temperate to submediterranean and then Mediterranean formations.

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655 JSC and GJM obtained funding for the development of this work. GJM, AGA and RSA
656 planned and conducted fieldwork, subsampled and described the sediments. JLT, HA and
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658 charcoal analyses. SM wrote the first draft of this article, assisted by LLM. JSC, LLM and
659 DSM, contributed with palaeoecological and geobotanical interpretations. All authors,
660 especially LLM, have revised and contributed to the final version of this manuscript and
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662

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988 **Figure captions**

989

990 **Figure 1.** Maps presenting biogeographical information of the study area. a) Iberian
 991 thermoclimatic belts (after Manzano *et al.*, 2017). b) Sierra Nevada thermoclimatic belts
 992 and lithology (Rams Sánchez, 2007; Valle, 1985, 2003), shading indicates calcareous and
 993 dolomitic substrates, while blank areas indicate siliceous materials (Delgado Calvo-Flores
 994 *et al.*, 2001; Rams Sánchez, 2007). The coring site (LdlMo) and other Sierra Nevada
 995 palaeoenvironmental records discussed in the text are indicated, as well as the Sierra
 996 Nevada National Park boundary. c) Vegetation units of the Sierra Nevada area (modified
 997 from REDIAM, Red de Información Ambiental de Andalucía, and own data).

998

999 **Figure 2.** Age-depth model and sedimentary log of the LdlMo lacustrine core. Records of
 1000 magnetic susceptibility, grain size mean, loss-on-ignition (LOI), Cladoceran heads,
 1001 *Daphnia* eggs and seed concentration are also included.

1002
 1003 **Figure 3.** Palynological (selected taxa) and charcoal diagram of the LdlMo lacustrine core
 1004 plotted in age. a) Trees, shrubs, nanophanerophytes and charcoal influx. b) Herbs, fungi,
 1005 ferns and aquatic taxa. Exaggeration curves ($\times 5$) are plotted in white. The complete
 1006 palynological diagrams plotted by age and by depth are available in Supplementary
 1007 Information 1 and 2.

1008
 1009 **Figure 4.** Chronology of the Holocene landscape changes in Sierra Nevada after the
 1010 LdlMo palaeoecological record. a) and b) Summer and winter insolation at 37°N (Laskar *et al.*,
 1011 2004). c) Percentage curves of likely cultivated taxa. d) Microcharcoal (10-125 μm)
 1012 influx. e) Percentage of coprophilous fungi. f) Grain size. g) Subalpine scrub abundance
 1013 (Brassicaceae, *Cytisus/Genista* type and *Juniperus*). h) Cryoromediterranean pastures
 1014 abundance (Caryophyllaceae, *Herniaria* and *Spergularia*). i) Percentages of deciduous
 1015 *Quercus*, evergreen *Quercus* and *Pinus sylvestris/nigra* type.

1016
 1017 **Figure 5.** Vegetation composition, structure and fire impact for the last ~8300 years in the
 1018 Sierra Nevada mountains after the palaeoecological record obtained from the LdlMo
 1019 lacustrine sequence. Inferred vegetation change mechanism, type of vegetation response,
 1020 and climatic/anthropogenic forcings are outlined.

1021

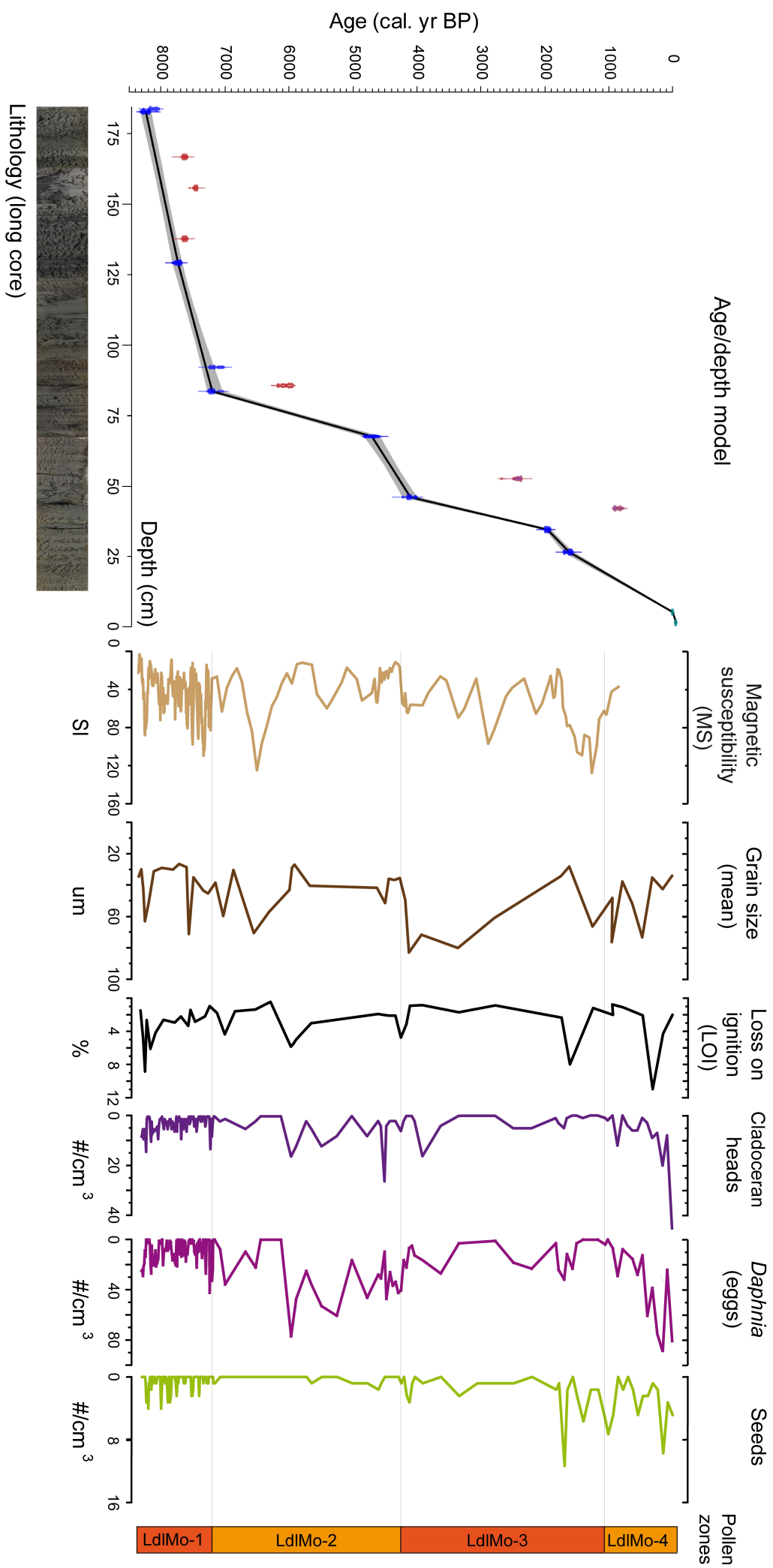
1022 TABLES

1023

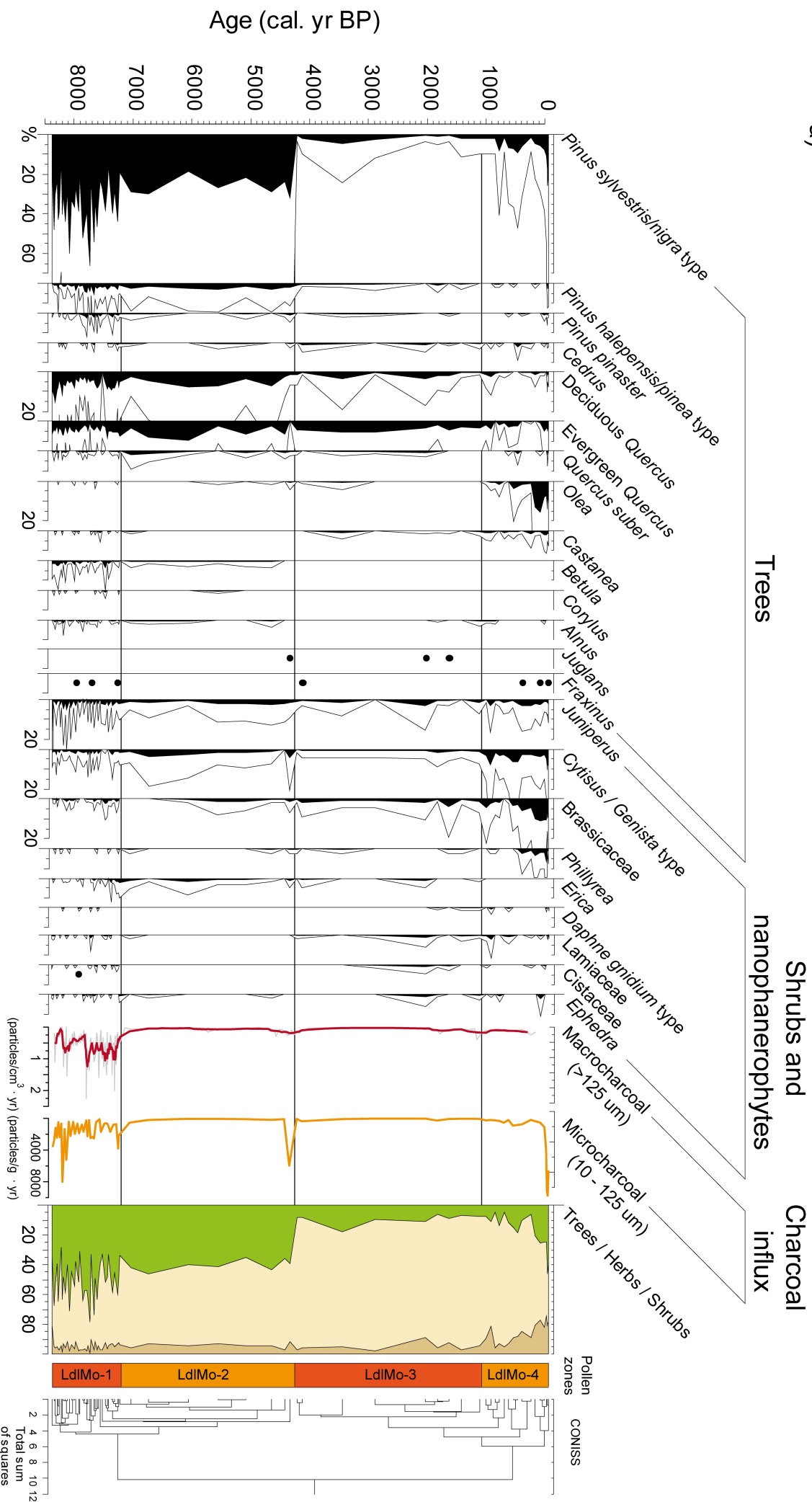
1024 **Table 1.** LdlMo Plutonium and radiocarbon dates.

Laboratory Code	Depth (cm)	Method	Material dated	Age (yr BP)	Calibrated age (cal. yr BP)	Median age (cal. yr BP)
	Surface	Present		-63 (AD 2013)		-63
	3,75	Plutonium	Bulk sediment	-13 (AD 1963)		-13
D-AMS 005126	25	14C	Bulk sediment	1700 \pm 29	1545-1696	1602
D-AMS 005127	33	14C	Bulk sediment	2003 \pm 21	1898-1994	1953
D-AMS 004807	40.5	14C	Plant	906 \pm 28	745-913	842**

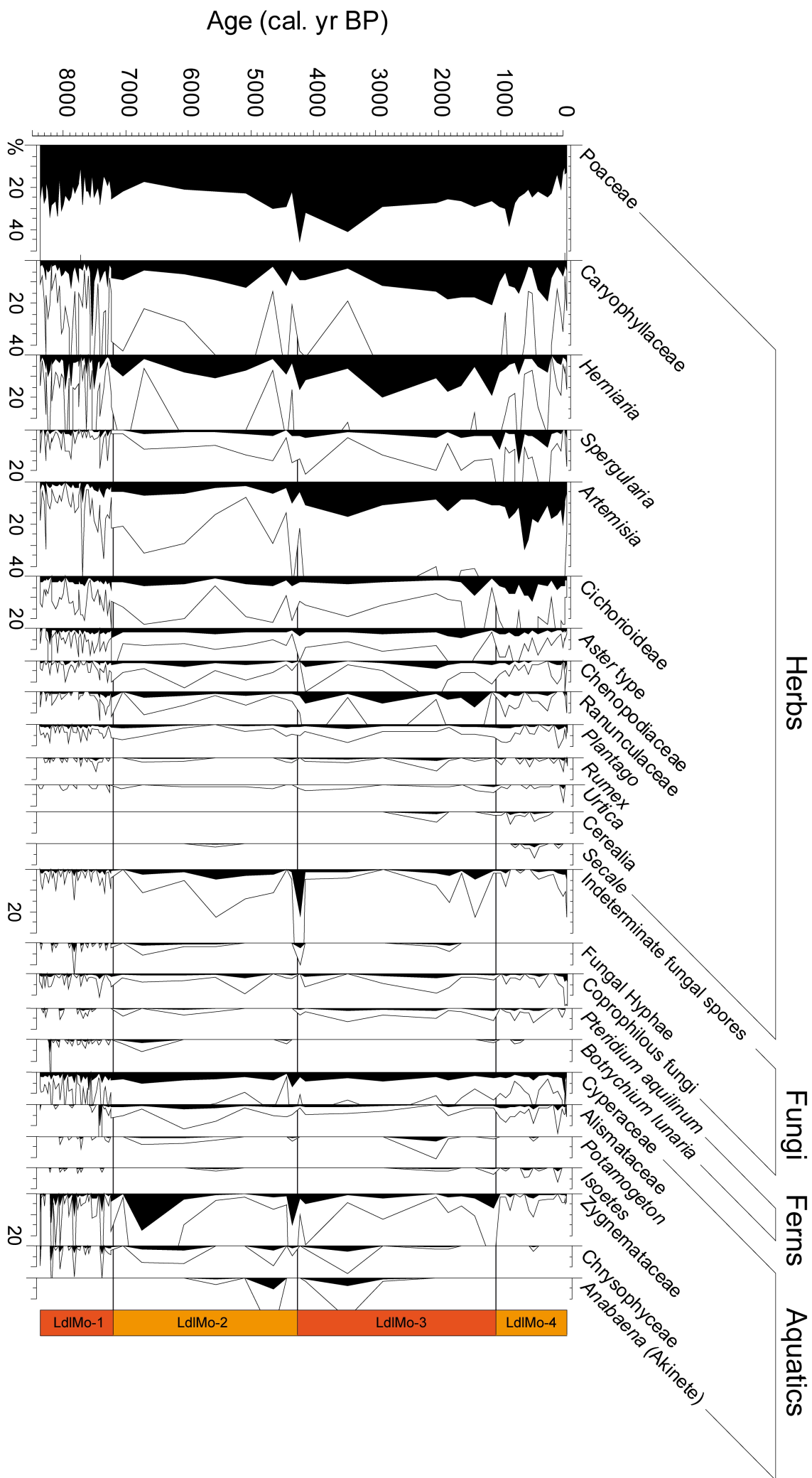
			Macrorremain			
D-AMS 005128	44.5	14C	Bulk sediment	3747 ± 30	3986-4161	4109
D-AMS 005129	51	14C	Bulk sediment	2375 ± 34	2337-2605	2405**
D-AMS 005130	66	14C	Bulk sediment	4153 ± 31	4578-4826	4698
D-AMS 005131	77	14C	Bulk sediment	29,671 ± 245	28,506-29,247	28,876**
D-AMS 005132	82	14C	Bulk sediment	6275 ± 40	7027-7113	7211
D-AMS 005133	84	14C	Bulk sediment	5256 ± 36	5928-6178	6019**
D-AMS 005134	90.5	14C	Bulk sediment	6229 ± 42	7008-7255	7155**
D-AMS 004379	127.5	14C	Bulk sediment	6910 ± 34	7674-7825	7736
D-AMS 004380	136	14C	Bulk sediment	6785 ± 43	7576-7683	7632
D-AMS 004381	154	14C	Bulk sediment	6548 ± 31	7422-7551	7456
D-AMS 004382	165	14C	Bulk sediment	6791 ± 41	7579-7684	7635
D-AMS 004383	181	14C	Bulk sediment	7403 ± 36	8168-8332	8250
D-AMS 004384	182	14C	Bulk sediment	7334 ± 38	8023-8284	8125
*Reimer <i>et al.</i> (2013), 95% confidence intervals. **Excluded from the age model.						

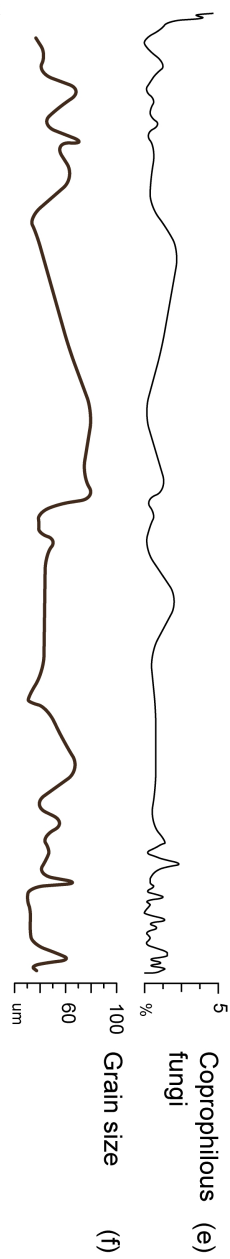
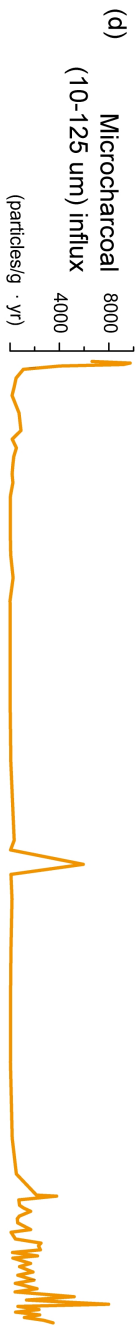
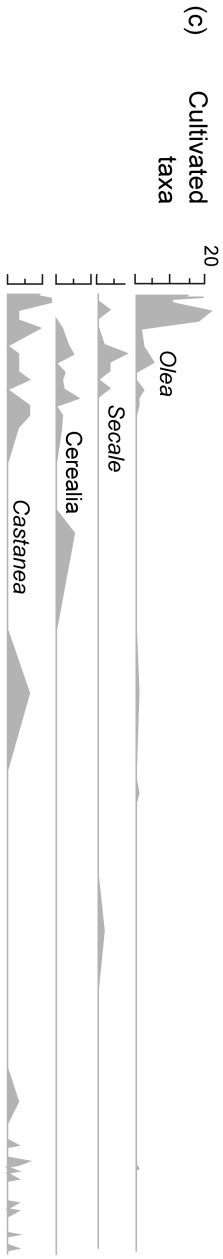
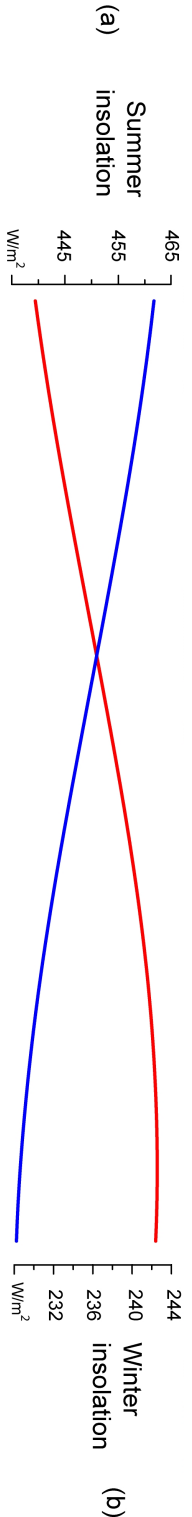


a)



b)





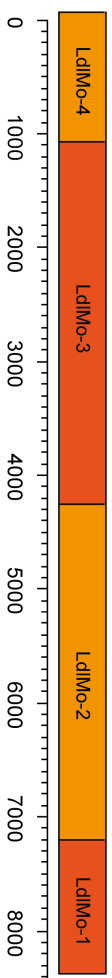
(g) *Juniperus*
Cytisus/Genista type
Brassicaceae

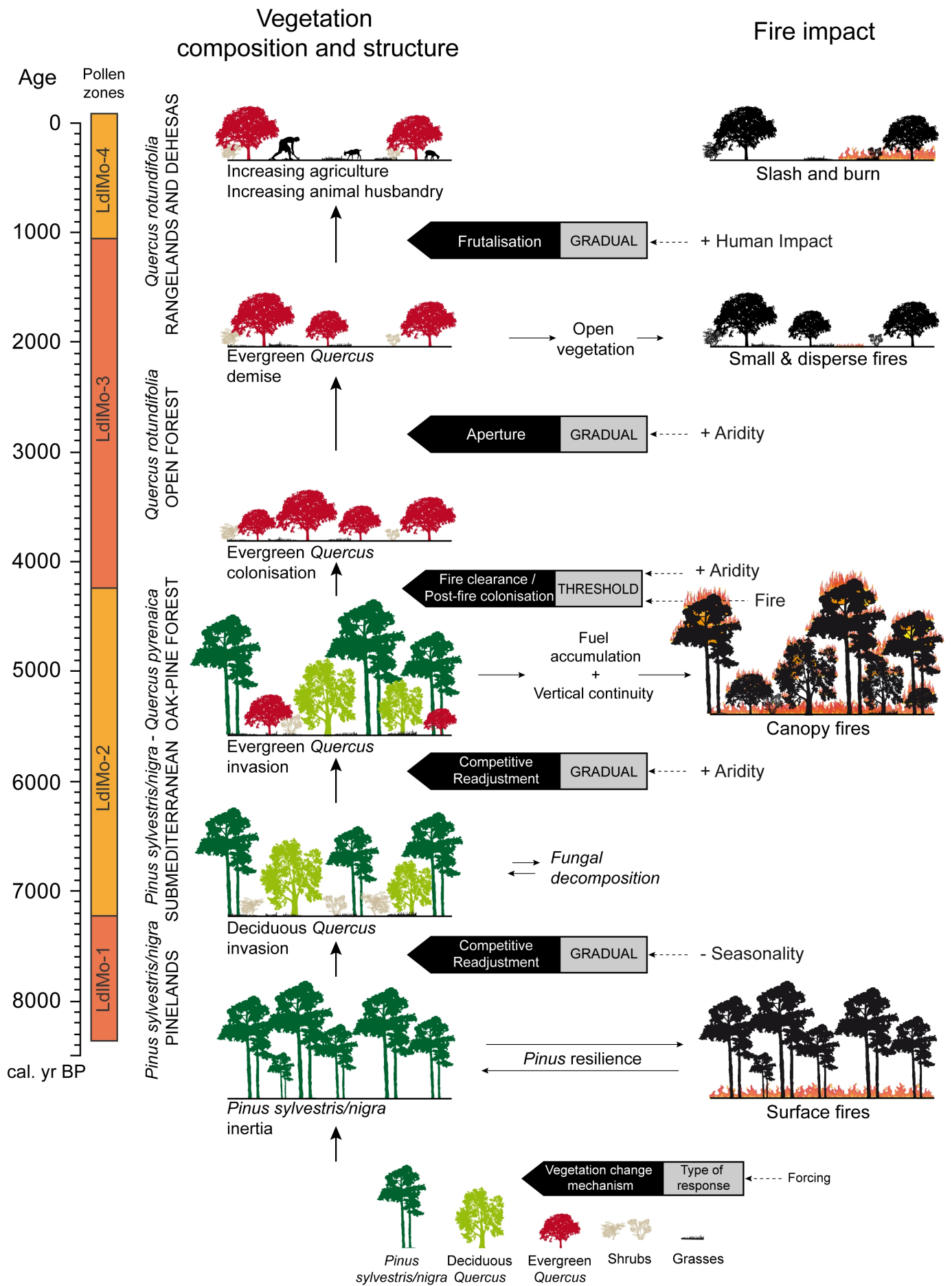
Caryophyllaceae /
Herniaria /
Spergularia /

(i) *Pinus sylvestris*/
nigra type
Evergreen
Quercus
Deciduous
Quercus

Pollen zones

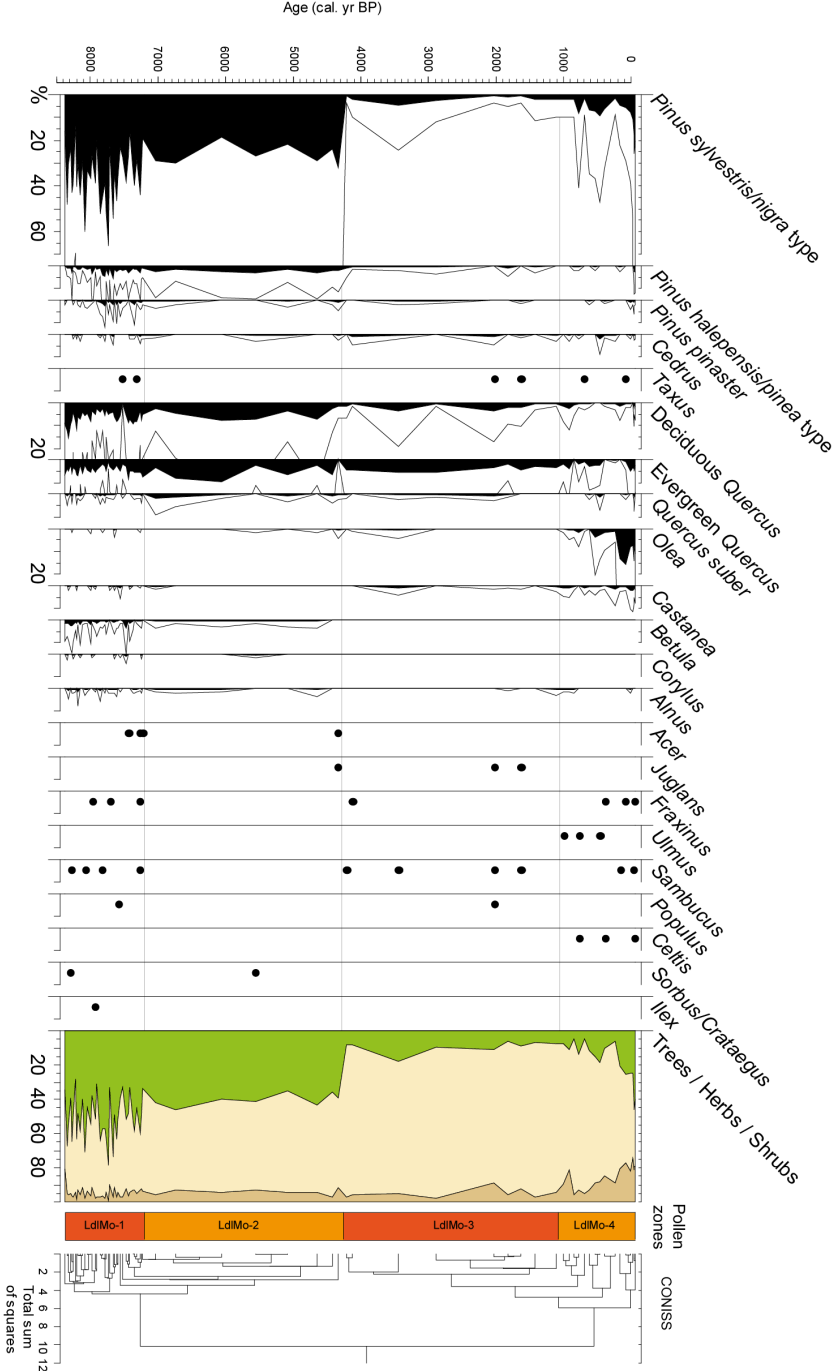
Age (cal. yr BP)



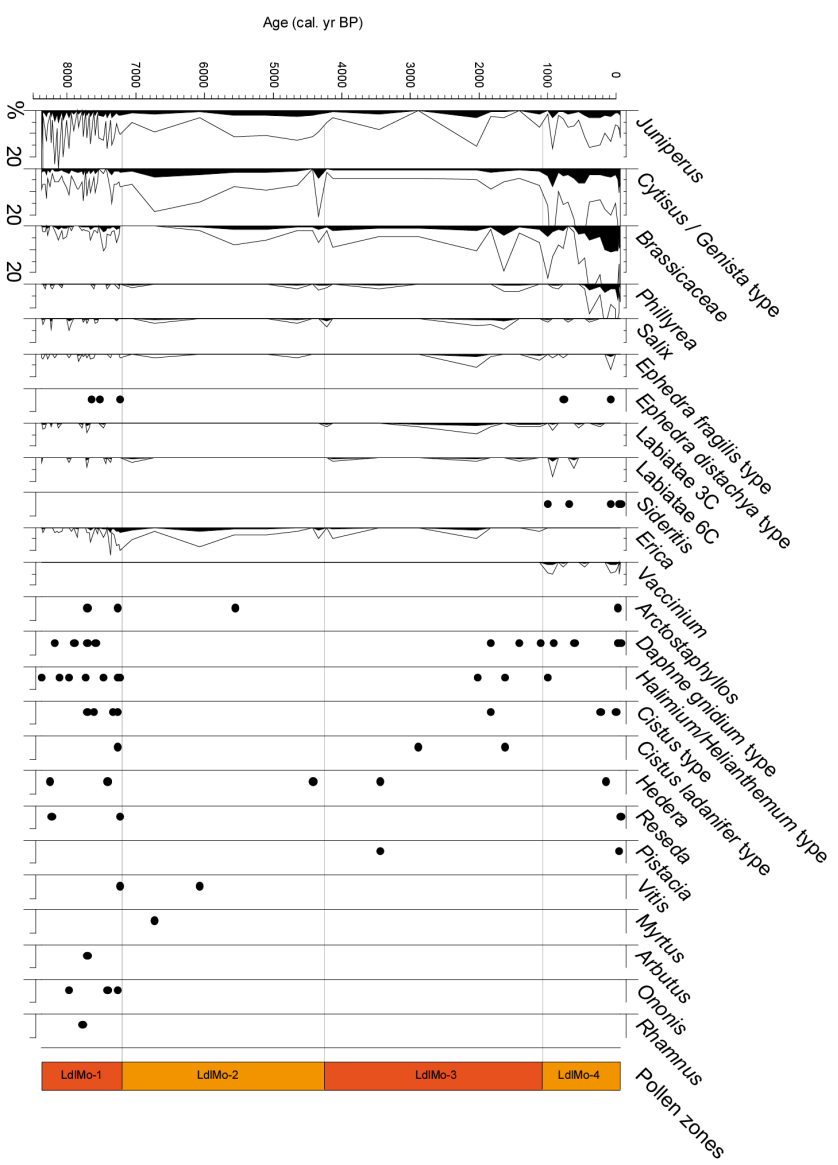


Supplementary Information 1. Complete palynological diagram plotted by age

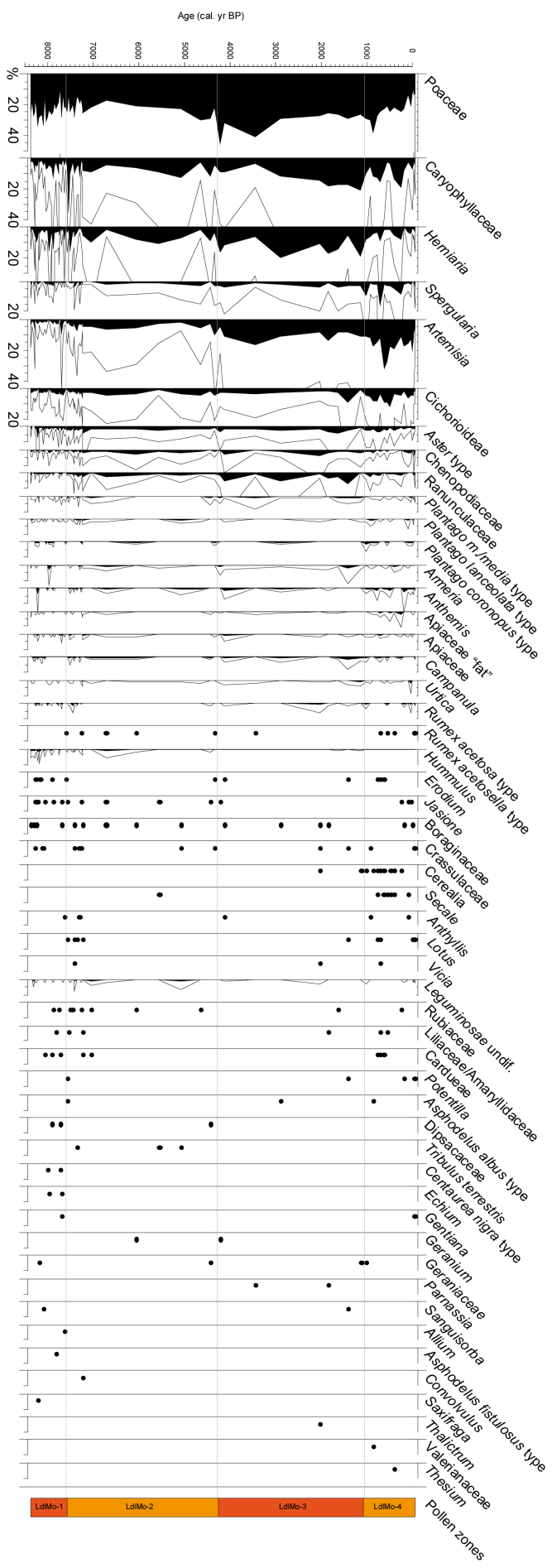
a) Trees



b) Shrubs and nanophanerophytes

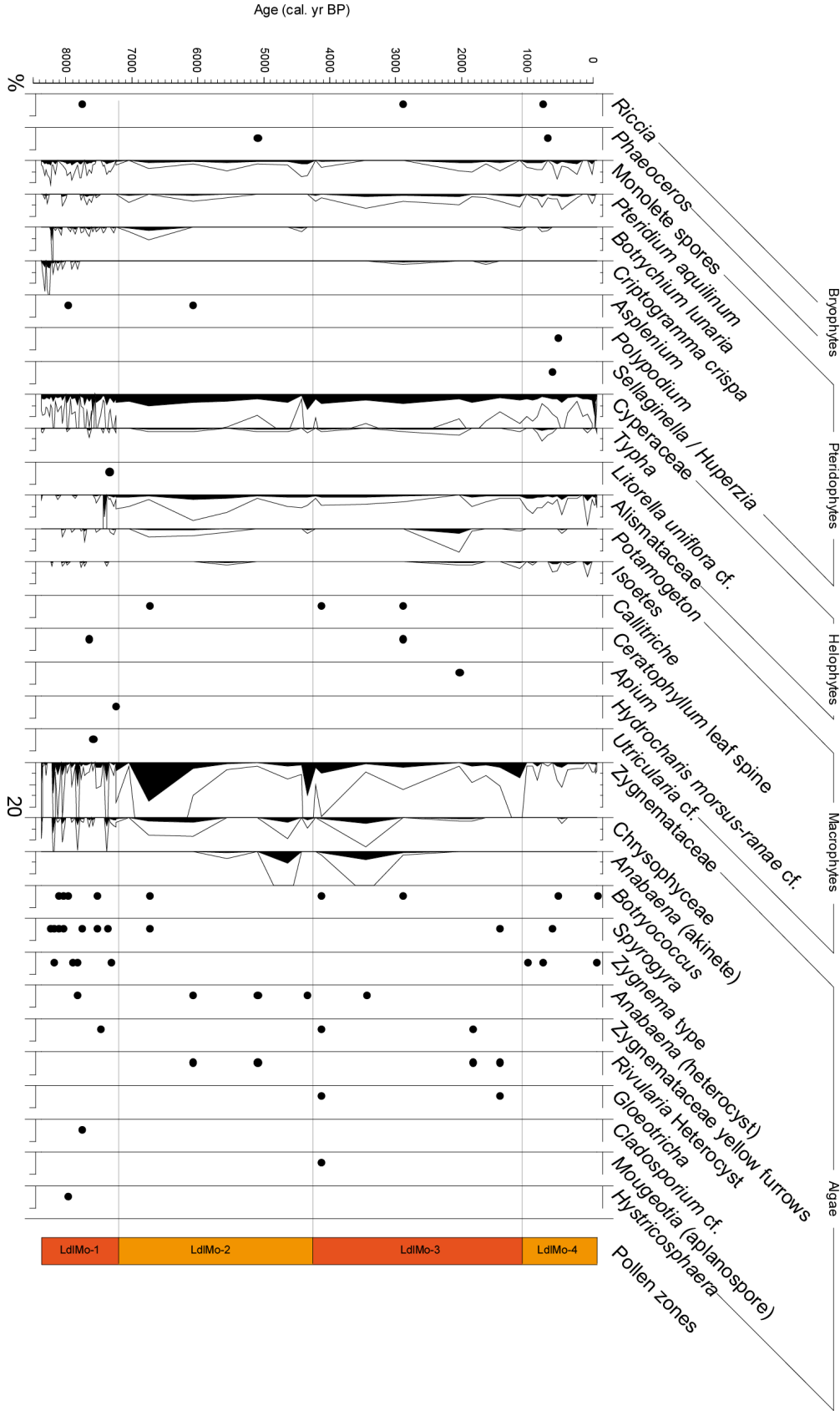


c) Herbs



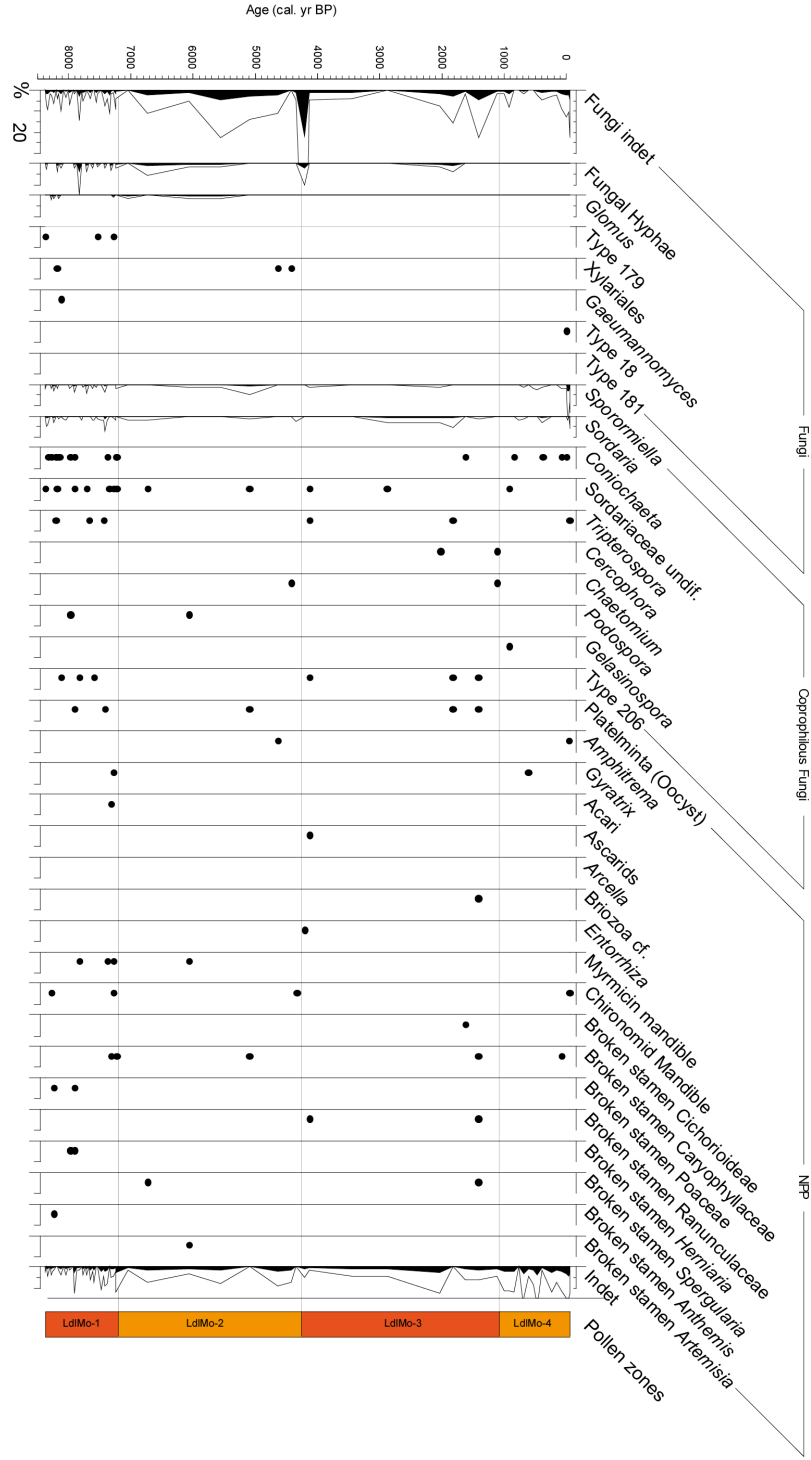
Supplementary Information 1. Complete palynological diagram plotted by age

d) Bryophytes, pteridophytes, helophytes, macrophytes and algae



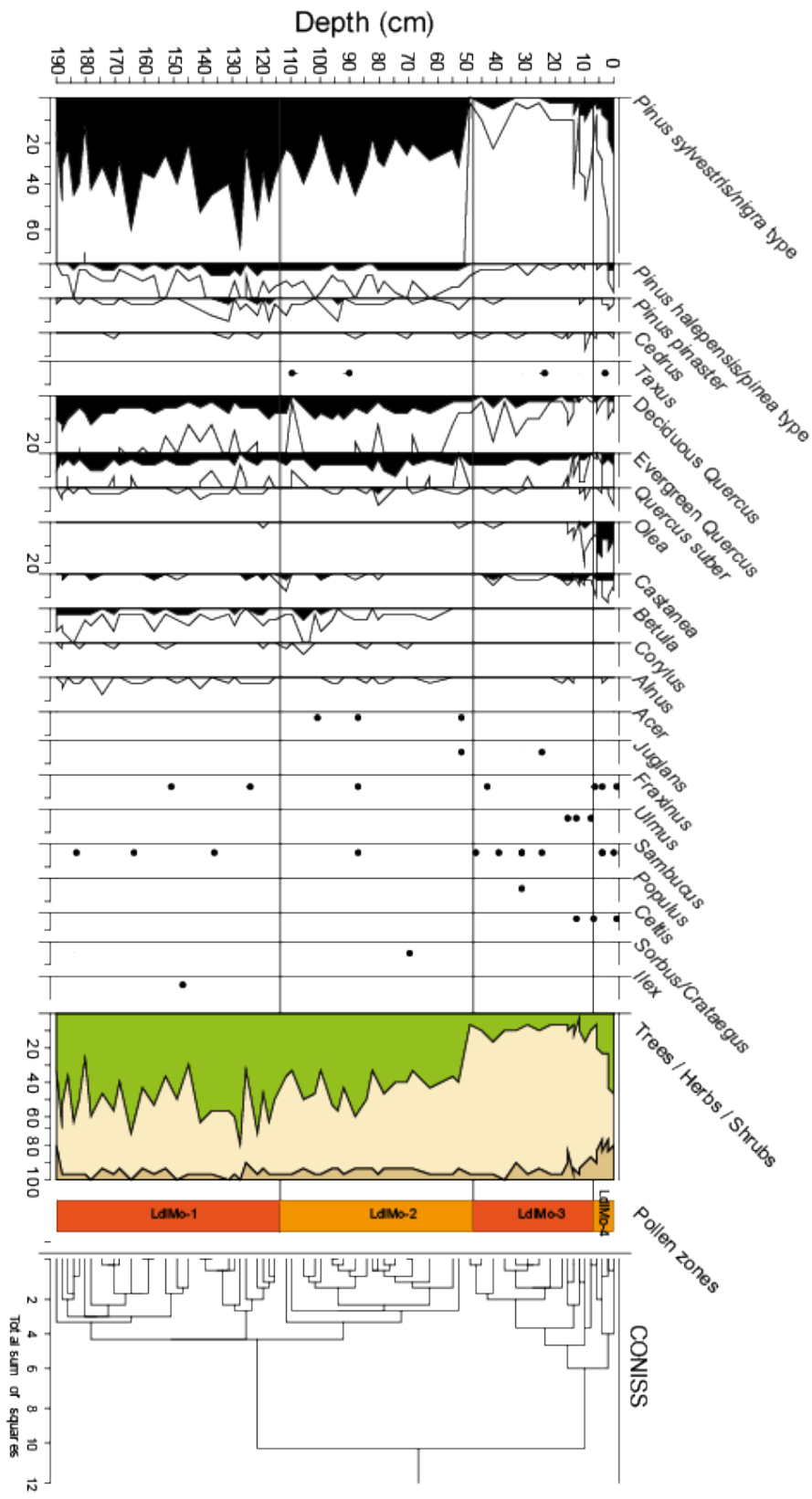
Supplementary Information 1. Complete palynological diagram plotted by age

e) Fungi and NPP



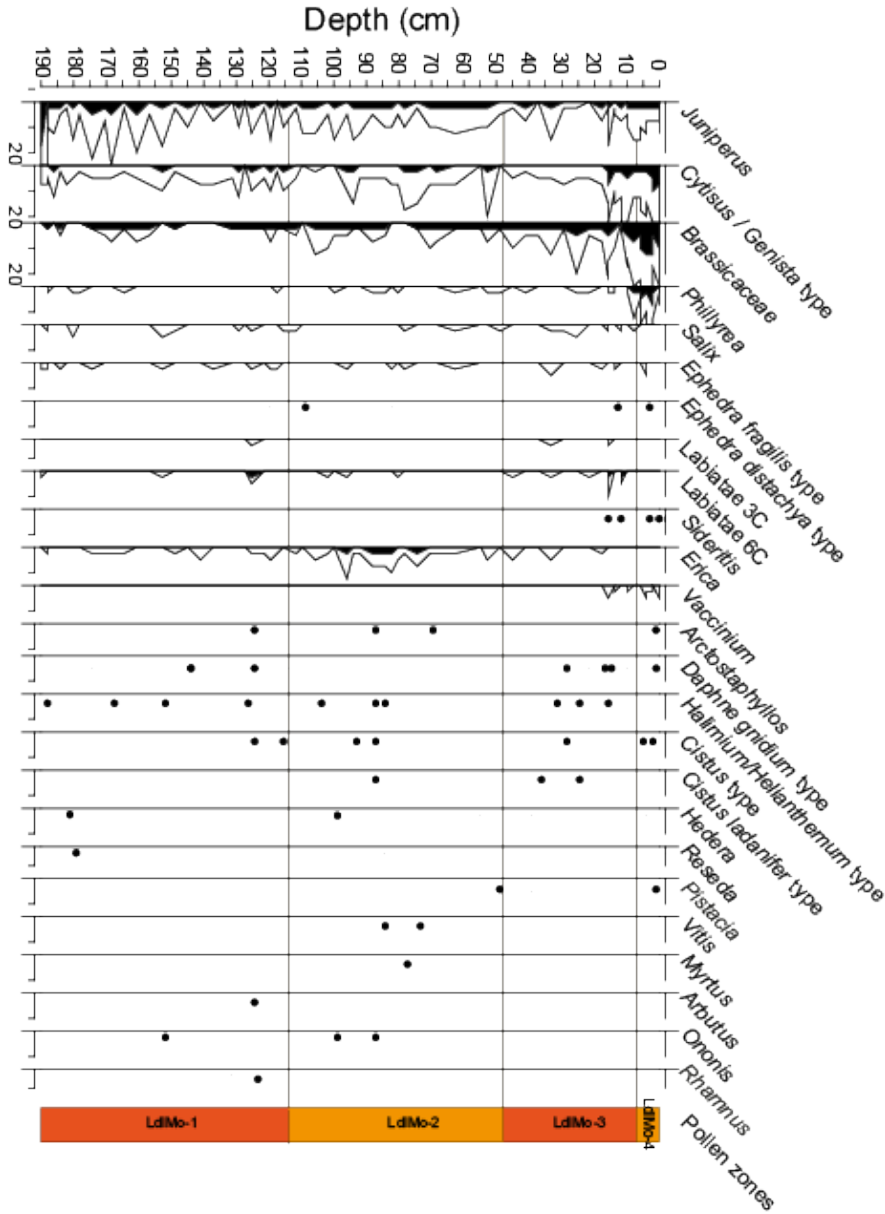
Supplementary Information 2. Complete palynological diagram plotted by depth

a) Trees



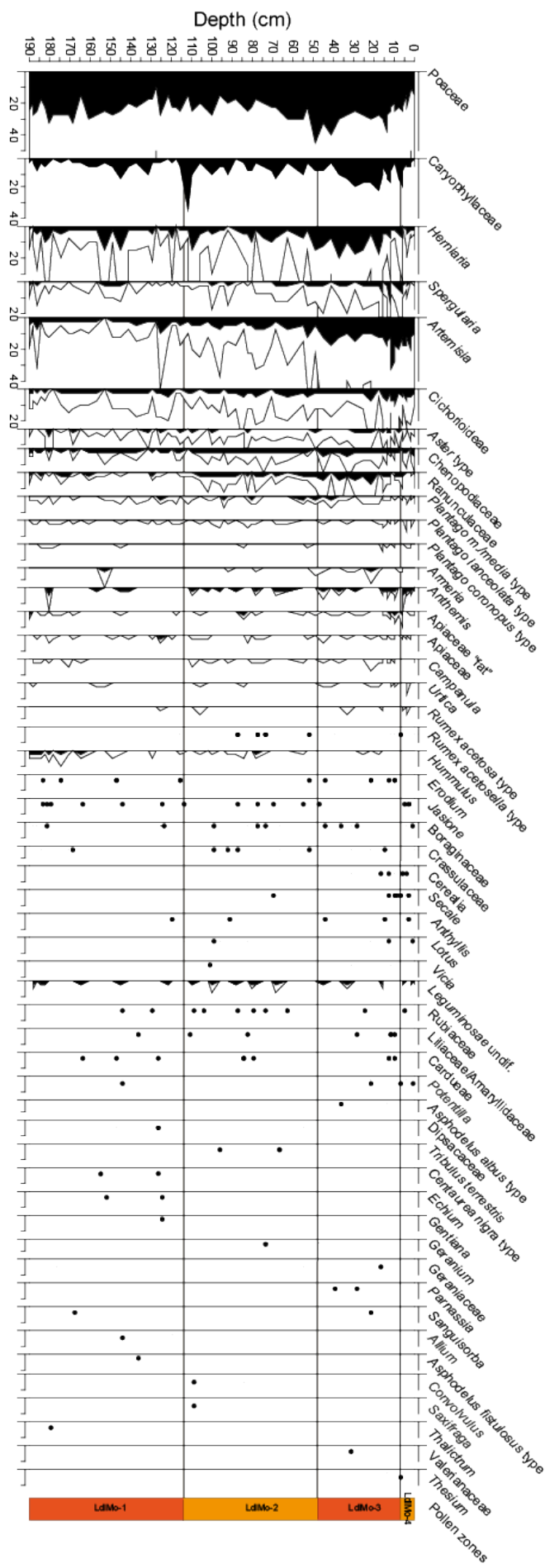
Supplementary Information 2. Complete palynological diagram plotted by depth

b) Shrubs and nanophanerophytes



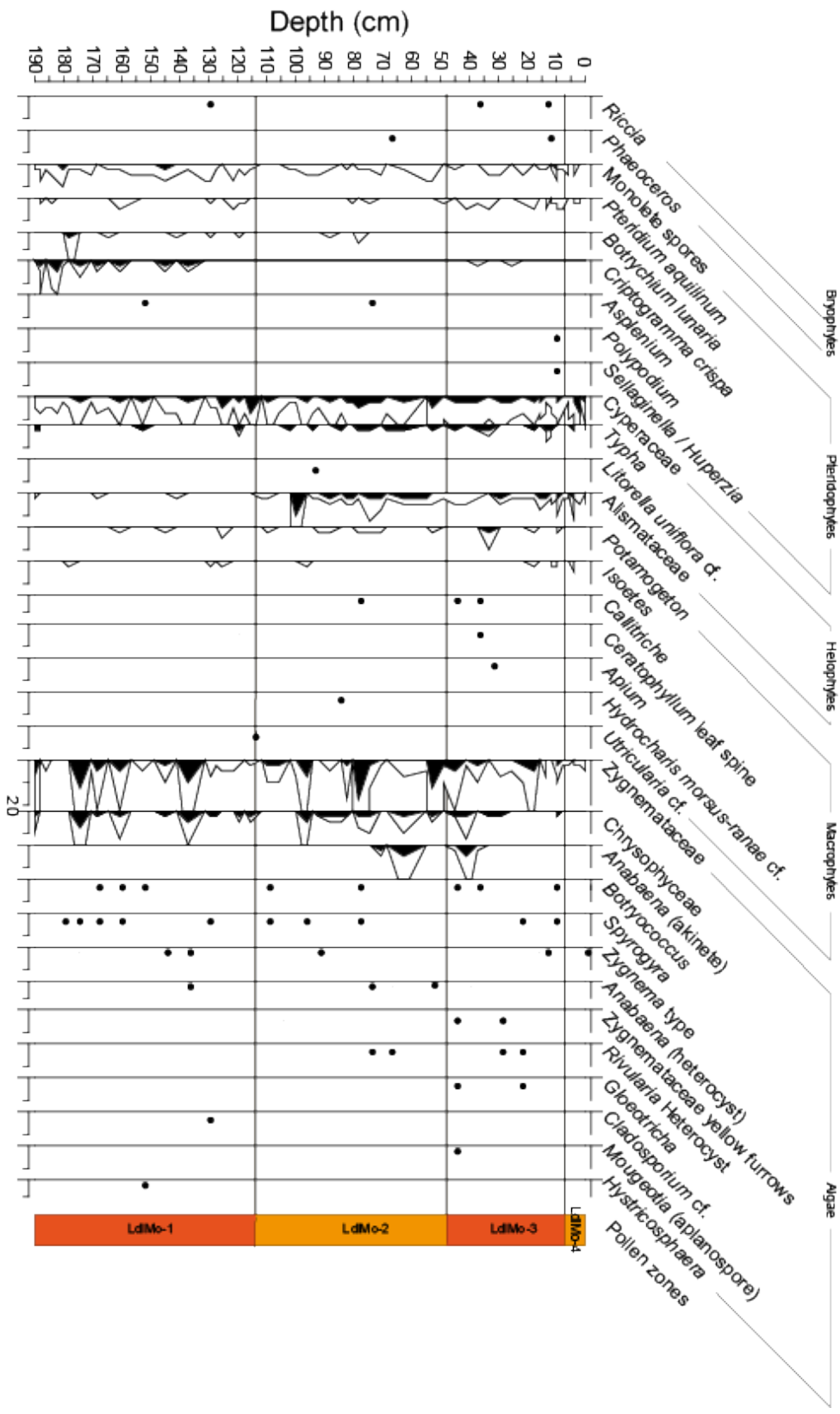
Supplementary Information 2. Complete palynological diagram plotted by depth

c) Herbs



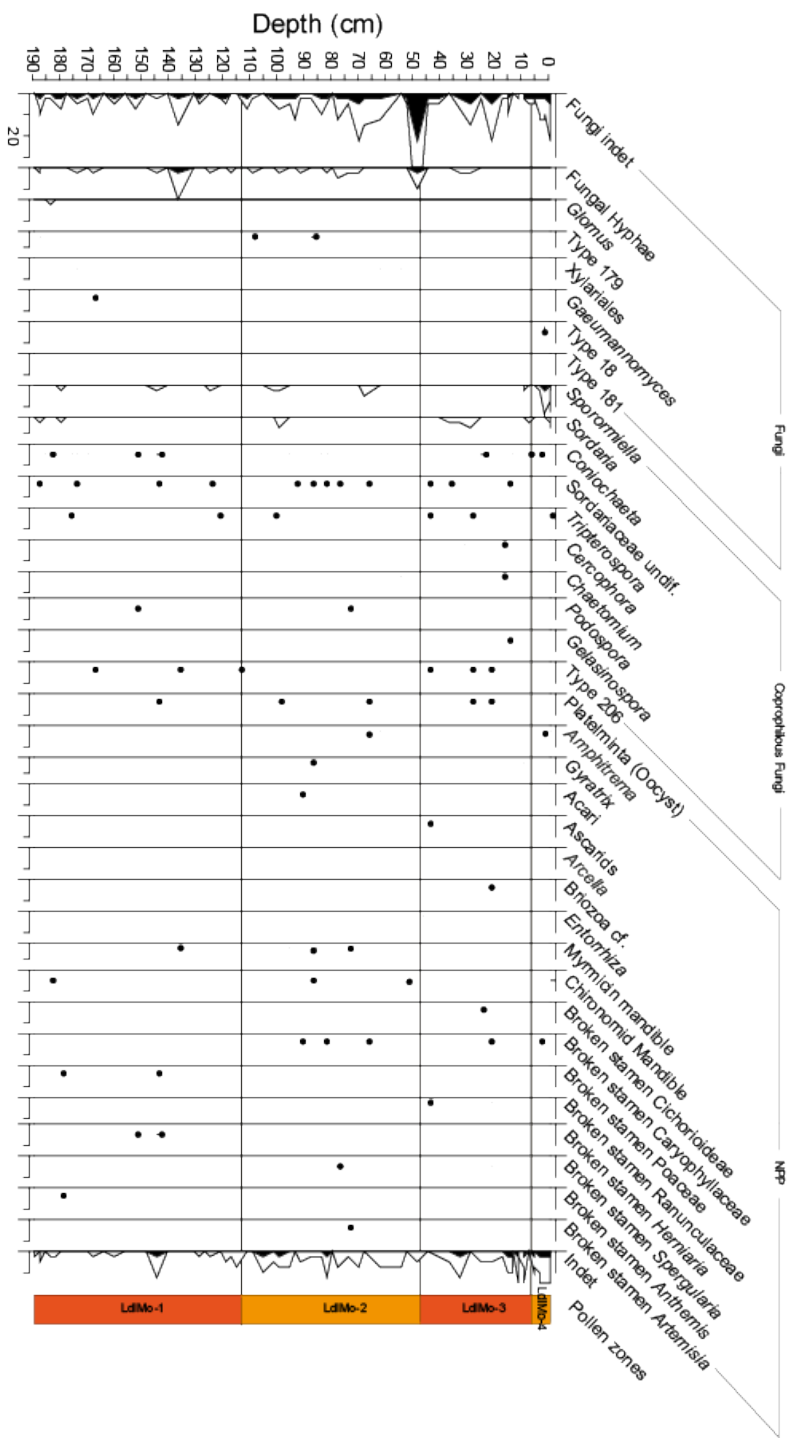
Supplementary Information 2. Complete palynological diagram plotted by depth

d) Bryophytes, pteridophytes, helophytes, macrophytes and algae



Supplementary Information 2. Complete palynological diagram plotted by depth

e) Fungi and NPP



Supplementary Information 3. Concentration diagram plotted by age (selected taxa)

